University of Alberta

Contribution of littoral and pelagic algal photosynthesis in Boreal Plain lakes.

by

Nicole Armstrong ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology
Department of Biological Sciences

Edmonton, Alberta

Fall 2000

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-59774-1

Canada

University of Alberta

Library Release Form

Name of Author: Nicole Armstrong

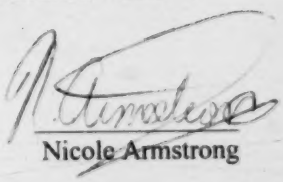
Title of Thesis: Contribution of littoral and pelagic algal photosynthesis in Boreal Plain lakes.

Degree: Master of Science

Year this Degree Granted: 2000

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell copies for private, scholarly, or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided, neither the thesis nor any substantial portion thereof may by printed or otherwise reproduced in any material form whatever without the author's written permission.



Nicole Armstrong

120 Luxton Avenue
Winnipeg, Manitoba
R2W 0L9

Date: _____

Abstract

Contribution of the littoral to whole-lake algal photosynthesis was studied in four lakes on the Boreal Plain in Alberta, Canada. In the littoral zone, rates of phytoplankton and epiphyton photosynthesis were positively related to algal biomass and total dissolved phosphorus concentration (r, 0.43-0.82, $P<0.001$). Relationships between macrophyte surface area and biomass were species-specific and could not be grouped based on dissected or entire leaf morphology. Lake-specific relationships between macrophyte surface area and biomass suggest that the amount of surface area available for epiphyton colonization is lake specific. Data collected from the study lakes and literature values from seven others were used to develop a relationship between littoral surface area and contribution to whole-lake algal photosynthesis ($r^2=0.90$, $P<0.0001$). Knowledge of the contribution of littoral and pelagic algal photosynthesis will aid in refining models that focus on landscape-water quality interactions in relatively flat and nutrient-rich environments, such as the Boreal Plain.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Contribution of littoral and pelagic algal photosynthesis in Boreal Plain lakes** submitted by **Nicole Armstrong** in partial fulfillment of the requirements for the degree of **Master of Science** in **Environmental Biology and Ecology.**

Dr. E.E. Prepas, Co-supervisor

Dr. D. Planas, Co-supervisor

Dr. E. Fee

Dr. B.G. Kotak

Dr. M. Loewen

Date: 11 Sept 2000

Acknowledgments

This research was conducted in partnership with the Network Centers of Excellence - Sustainable Forest Management (SFM-NCE) and Terrestrial and Riparian, Organisms, Lakes and Streams (TROLS) within the forest management areas of Alberta-Pacific Forest Industries, Inc. and Weyerhaeuser Canada, Ltd. Finacial support to these programs included the following sources: Natural Sciences and Engineering Research Council of Canada (NSERC) (including Collaborative Special Projects and University-Industry grants to E.E. Prepas and 11 co-Principal Investigators); Alberta Environmental Protection; Alberta Economic and Tourist Development; Alberta-Pacific Forest Industries; Manning Diversified Forest Products; Weyerhaeuser Canada Ltd; University of Alberta; Employment Canada; National Research Council of Canada Industrial Research Assistantship Program; National Water Research Institute; Ainsworth Lumber Company; Syncrude Canada Ltd; C & S Resources; and R L & L Consulting and NSERC research grants to Drs. Prepas and Planas. Funding was also provided by a Post-Graduate NSERC Scholarship and the Circumpolar Institute (Canadian Boreal Alberta Research grant).

Water chemistry analyses were done at the University of Alberta's Limnology Laboratory and Meanook Biological Research Station. Logistical support or intellectual advice was provided by E. Allen, B. Alison, R. Bernier, S. Blair, S. Block, J. Burke, N. Carmosini, T. Charette, M. Dance, Dr. P. Dinsmore, K. Gibson, M. Keohane, S. Manchur, T. Morcos, K. Murie, C. Nahorniak, S. Nicopolous, S. Paquet, S. Reedyk, G. Sandland, N. Scott, M. Serediak, Dr. G. Scrimgeour, P. Siwik,

K. Westcott, J. White, I. Whitson, and W. Zyla. Special thanks to Andrew Hamilton for field and laboratory assistance.

I am especially grateful for the support and guidance of my two supervisors, Drs. D. Planas and E. Prepas, and my supervisory committee members, Drs. E. Fee, M. Hickman and B. Kotak, throughout this study. Thank you to Dr. G. Robinson for much needed encouragement and inspiration before and during this project. Thank you to the many colleagues at the University of Alberta who provided friendship, support and advice, in particular, Anne Forshner, Natalie McMaster, Cherie Westbrook and Maggie Xenopolous. Thank you to all my friends and family, especially my parents and Nicolas, Geoff, Bonnie and Michael.

Table of Contents

Chapter One Background to Study....1

1.0 Introduction....2
1.1 Background....2
1.2 Summary and Research Objectives....5
1.3 References....8

Chapter Two Relationship between surface area and biomass of submersed macrophytes in lakes....13

2.0 Introduction....14
2.1 Methods....15
2.1.1 Study site and sample collection....15
2.1.2 Estimation of macrophyte surface area and dry weight....16
2.1.3 Study lake physical, chemical and biological characteristics....17
2.1.4 Statistical analyses....19
2.2 Results....20
2.3 Discussion....22
2.4 References....26

Chapter Three Relative contribution of littoral and pelagic algae to whole-lake algal photosynthesis in eutrophic lakes....37

3.0 Introduction....38
3.1 Methods....40
3.1.1 Study sites....40
2.1.2 Sampling....41
3.1.3 Chemical analyses....42
3.1.4 Algal analysis....43
3.1.5 Macroinvertebrates....45
3.1.6 TROLS sampling....46
3.1.7 Statistical analyses....47
3.2 Results....48
3.3 Discussion....55
3.4 References....64

Chapter Four Synthesis....83

4.0 Synthesis....84
4.1 References....87

Appendix A Estimation of macrophyte biomass and surface area....88

A.0 Estimation of macrophyte biomass.....89
A.1 Estimation of macrophyte surface area.....90

Appendix B Epiphyton photosynthesis-irradiance curves.....91

Appendix C Phytoplankton photosynthesis-irradiance curves.....108

List of Tables

Chapter 2

Table 2.1: Morphological characteristics and presence/absence of the six macrophyte species in the study lakes.....28

Table 2.2: Mean summer general chemical, biological and physical characteristics of the study lakes.....29

Table 2.3: Comparison of the dry weight of Long Lake macrophyte species dipped in dye and those without immersion in dye (P = probability).....30

Table 2.4: Regression parameters for the relationship between macrophyte surface area (dependent variable cm^2) and biomass (independent variable g dry weight) for each species in the study lakes (± SE).....31

Table 2.5: Probability values from an ANCOVA comparing both the slope and intercept of the relationship between macrophyte surface area (dependent variable) and biomass (independent variable) between species (independent variable). 32

Table 2.6: Probability values from an ANCOVA comparing both the slope and intercept of the relationship between macrophyte surface area (dependent variable) and biomass (independent variable) between lakes (independent variable) for each macrophyte species.....33

Chapter 3

Table 3.1: Drainage basin and lake characteristics (E.E. Prepas, unpublished), and mean August macrophyte density.....68

Table 3.2: Median and range (in parenthesis) of summer littoral nutrient concentrations, phytoplankton and epiphyton chl*a* concentration and light extinction in the study lakes (n = 24 per lake).....69

Table 3.3: Median and range (in parenthesis) of summer pelagic nutrient concentrations, phytoplankton chl*a* concentration and light extinction in the study lakes (Except E_{PAR} (n = 4), n = 24 per lake).....70

Table 3.4: Median and range (in parenthesis) of nutrient concentrations, algal parameters and light extinction in the study lakes during periods of mixing (n = 30) and stratification (n = 96).....71

Table 3.5: Results of a nested ANOVA examining spatial and temporal variations in epiphyton biomass in the study lakes (% = percent variance component estimate).....72

Table 3.6: Mean summer pelagic and littoral phytoplankton photosynthesis (areal $mgC \cdot m^{-2} \cdot d^{-1}$ and volumetric $mgC \cdot m^{-3} \cdot d^{-1}$).....73

Table 3.7: Median chl*a* normalized maximum optimal rate of photosynthesis ($Pmax_b$ $mgC \cdot mgChla^{-1} \cdot h^{-1}$) and efficiency of photosynthesis ($alpha_b$ $mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$) for littoral and pelagic phytoplankton, and epiphyton (with range in parenthesis).....74

Table 3.8: Spearman rank correlation coefficients between epiphyton or phytoplankton mean daily photosynthesis and light extinction, water chemistry variables, and epiphyton and phytoplankton biomass (n = 86 except for PN and TN where n = 67).....75

Table 3.9: Spearman rank correlation coefficients between epiphyton mean daily photosynthesis and light extinction, water chemistry variables, and epiphyton and phytoplankton biomass (n = 61 in stratified, n = 28 in mixed).....76

Table 3.10: Data obtained and derived from the study and literature lakes (values derived for this study are in bold).....77

List of Figures

Chapter 1

Figure 1.1: Map of Alberta and the study lakes.....12

Chapter 2

Figure 2.1: *P. richardsonii* and *P. zosteriformis* surface area related to biomass and least squares regression line.....34

Figure 2.2: *C. demersum* surface area related to biomass and least squares regression line.....35

Figure 2.3: *M. exalbescens* surface area related to biomass and least squares regression line.....36

Chapter 3

Figure 3.1: Schematic of the Nitex-Plexiglas rings.....78

Figure 3.2: Seasonal changes in phytoplankton photosynthesis and biomass in the study lakes.....79

Figure 3.3: Seasonal changes in epiphyton photosynthesis and biomass in the study lakes with Spearman's rank correlation.....80

Figure 3.4: Contribution of epiphyton and both littoral and pelagic phytoplankton to whole-lake algal photosynthesis in the study lakes.....81

Figure 3.5: Plot of percent littoral contribution to whole-lake algal photosynthesis and surface area for 11 lakes with least squares regression line.....82

Appendix B

Figure B1: Epiphyton photosynthesis-irradiance curves in SPH 20 (June 1998).....92

Figure B2: Epiphyton photosynthesis-irradiance curves in SPH 100 (June 1998).....93

Figure B3: Epiphyton photosynthesis-irradiance curves in SPH 200 (June 1998).....94

Figure B4: Epiphyton photosynthesis-irradiance curves in SPH 800 (June 1998).....95

Figure B5: Epiphyton photosynthesis-irradiance curves in SPH 20 (July 1998).....96

Figure B6: Epiphyton photosynthesis-irradiance curves in SPH 100 (July 1998).....97

Figure B7: Epiphyton photosynthesis-irradiance curves in SPH 200 (July 1998).....98

Figure B8: Epiphyton photosynthesis-irradiance curves in SPH 800 (July 1998).....99

Figure B9: Epiphyton photosynthesis-irradiance curves in SPH 20 (August 1998).....100

Figure B10: Epiphyton photosynthesis-irradiance curves in SPH 100 (August 1998).....101

Figure B11: Epiphyton photosynthesis-irradiance curves in SPH 200 (August 1998).....102

Figure B12: Epiphyton photosynthesis-irradiance curves in SPH 800 (August 1998).....103

Figure B13: Epiphyton photosynthesis-irradiance curves in SPH 20 (September 1998).....104

Figure B14: Epiphyton photosynthesis-irradiance curves in SPH 100 (September 1998).....105

Figure B15: Epiphyton photosynthesis-irradiance curves in SPH 200 (September 1998).....106

Figure B16: Epiphyton photosynthesis-irradiance curves in SPH 800 (September 1998).....107

Appendix C

Figure C1: Phytoplankton photosynthesis-irradiance curves in SPH 20 (June 1998).....109

Figure C2: Phytoplankton photosynthesis-irradiance curves in SPH 100 (June 1998).....110

Figure C3: Phytoplankton photosynthesis-irradiance curves in SPH 200 (June 1998).....111

Figure C4: Phytoplankton photosynthesis-irradiance curves in SPH 800 (June 1998).....112

Figure C5: Phytoplankton photosynthesis-irradiance curves in SPH 20 (July 1998).....113

Figure C6: Phytoplankton photosynthesis-irradiance curves in SPH 100 (July 1998).....114

Figure C7: Phytoplankton photosynthesis-irradiance curves in SPH 200 (July 1998).....115

Figure C8: Phytoplankton photosynthesis-irradiance curves in SPH 800 (July 1998).....116

Figure C9: Phytoplankton photosynthesis-irradiance curves in SPH 20 (August 1998).....117

Figure C10: Phytoplankton photosynthesis-irradiance curves in SPH 100 (August 1998).....118

Figure C11: Phytoplankton photosynthesis-irradiance curves in SPH 200 (August 1998).....119

Figure C12: Phytoplankton photosynthesis-irradiance curves in SPH 800 (August 1998).....120

Figure C13: Phytoplankton photosynthesis-irradiance curves in SPH 20 (September 1998).....121

Figure C14: Phytoplankton photosynthesis-irradiance curves in SPH 100 (September 1998).....122

Figure C15: Phytoplankton photosynthesis-irradiance curves in SPH 200 (September 1998).....123

Figure C16: Phytoplankton photosynthesis-irradiance curves in SPH 800 (September 1998).....124

Chapter One: Background to Study

1.0 Introduction

Littoral algae, i.e. those living in the interface zone between the highest seasonal water level and the maximum depth of macrophyte colonization, play a critical role in lakes. Whereas free-floating algae (phytoplankton) inhabit both the littoral and pelagic (open water) zones, epiphyton (algae attached to macrophytes) are present only in the littoral. Littoral algae provide an important carbon source for consumers including dipterans, oligochaetes, gastropods, hydracarinids, coleopterans, trichopterans, amphipods, tadpoles and fish (Cattaneo and Mousseau 1995, France 1995). Littoral food webs appear to be uncoupled from those in the pelagic (France 1995), and can provide larger contributions to photosynthesis than primary producers in pelagic food webs (Jenkerson and Hickman 1986, Wetzel et al. 1972). Wetzel (1990) suggests that epiphytic algae are both major contributors to algal photosynthesis and primary regulators of nutrient fluxes in lakes. Attached algae are characterized by a high efficiency of nutrient recycling and retention within the periphytic mat (Wetzel 1996) and may be provided with supplemental nutrients from their substrata (Hansson 1988). In contrast, phytoplankton benefit from circulation through the water column which provides a continual source of nutrients, and from greater access to light than periphyton (Hansson 1988). Littoral algae may also influence macrophyte biomass and distribution through competition for nutrients and light (Phillips et al. 1978). Due to the location of the littoral zone at the interface between the main body of the lake and the shoreline, littoral algae may respond rapidly to pollutant inputs (Raspopov et al. 1996) providing an initial indicator of aquatic ecosystem response to disturbance. Thus, littoral algae are crucial to both function and understanding in lakes.

1.1 Background

Studies of algal photosynthesis in lakes have traditionally focused on pelagic phytoplankton. Total phosphorus (TP), total nitrogen (TN), and phytoplankton biomass generally correlate with rates of pelagic phytoplankton photosynthesis (Schindler 1978, Smith 1980). However, little is known about photosynthetic rates of epiphyton and thus their role may be greatly underestimated. Rates of epiphyton photosynthesis may not correlate with nutrient concentrations or other variables such light extinction. A number of studies have shown that chemical and physical conditions within the epiphytic mat can differ substantially from the immediate surroundings (Riber and Wetzel 1987). As a result, studies of epiphyton photosynthetic rates have focused primarily on correlation with biomass (Kairesalo 1980, Jenkerson and Hickman 1983, Jones 1984, Muller 1995) although relationships with temperature, light, nutrients and grazing pressure (Stevenson et al. 1996) may also be expected. Higher nutrient competition and reduced light penetration within the epiphytic mat may reflect high cell densities (Kairesalo 1980, Riber et al. 1984, Meulemans 1988, Muller 1995) as compared to free-floating algae. Complex interactions between epiphytes and their macrophyte substrata (Wetzel 1983b, Harrison and Durance 1985, Burkholder and Wetzel 1985) may further obscure relationships with water column variables. Epiphyton not only receive less attention than phytoplankton, but relationships with biogeochemical variables are less direct.

Epiphyton are often overlooked due to their heterogeneous distribution (Wetzel 1983a) and the numerous methodological difficulties associated with sampling. Morin and Cattaneo (1992) suggest that ability to detect patterns in attached algal ecology is limited due to the large sample sizes required to overcome high replicate variability. In

addition, separating epiphyton from the macrophyte substrata is difficult (Cattaneo and Kalff 1978) and therefore, artificial substrata are often used. Although estimates of chlorophyll *a* are less variable on artificial substrata (Morin and Cattaneo 1992), its use ignores potential interactions between macrophyte and epiphyte. However, the degree of positive macrophyte-epiphyte interaction depends on the nutrient content of the water such that interactions are likely important in oligotrophic lakes and minimal in eutrophic lakes (Eminson and Moss 1980). A tendency to disregard epiphyton contributes to a lack of knowledge regarding relationships between photosynthetic rates and biogeochemical variables.

To determine the contribution of epiphyton to whole-lake algal photosynthesis, quantitative assessment of macrophyte surface area available for colonization is necessary. Estimates of macrophyte biomass are readily available in the literature and relationships with littoral slope (Duarte and Kalff 1986), nutrients (Phillips et al. 1978), light quality (Chambers and Prepas 1988) and quantity (Chambers and Kalff 1985) have been derived. In contrast, measurements of macrophyte surface area are rare and laborious, involving colorimetric techniques (Cattaneo and Carignan 1983, Watala and Watala 1994), image analysis (Gerber et al. 1994) and physical assessment of leaf area (Spence et al. 1973, Brown and Manny 1985). Currently, little is known about potential relationships between macrophyte surface area and biogeochemical variables. Although estimates of specific leaf area ($cm^2 \cdot g^{-1}$ dry weight) exist (Spence et al. 1973), data for stems is absent. Sher-Kaul et al. (1995) examined relationships between surface area and biomass of whole macrophyte plants in Lake Geneva and suggested that species-specific differences were not related to leaf morphology. Despite potential for correlation

between macrophyte surface area and biomass, there is an absence of general relationships in the literature.

Previous research suggests that the contribution of littoral algae to whole-lake algal photosynthesis depends on lake morphometry, and both macrophyte density and areal distribution (Kairesalo 1980, Jenkerson and Hickman 1986). Shallow lakes with dense macrophyte beds provide an opportunity for littoral algal photosynthesis to exceed that in the pelagic. Since the proportion of littoral surface area relative to the pelagic depends on lake morphometry and macrophyte distribution, a relationship with littoral contribution to algal photosynthesis is expected.

Of studies comparing littoral and pelagic contributions to algal photosynthesis, most have focused on lakes where pelagic, rather than littoral, algal photosynthesis dominates (Sondergaard and Sand-Jensen 1978, Kairesalo 1980, Allen and Ocevski 1981, Jones 1984, Gessner et al. 1996). Typically, these studies contrast pelagic phytoplankton and epiphyton photosynthesis and rarely are estimates of littoral phytoplankton photosynthesis included (Allen and Ocevski 1981, Gessner et al. 1996). However, phytoplankton photosynthesis may vary due to differences in biomass, water temperature (James and Barko 1991) and competition (Phillips et al. 1978, Wetzel 1983a, Hansson 1990) within the littoral and pelagic zones. Previous studies of littoral and pelagic algae are based on a wide range of methodologies for epiphyton sampling and measurements of photosynthesis that are characterized by different sources of error (Harris 1978, Wetzel 1983b). Future determination of the variables influencing the relative contribution of phytoplankton and epiphyton to whole-lake algal photosynthesis would benefit from consistent methodology in both littoral and pelagic dominated lakes.

1.2 Summary and Research Objectives

Shallow and nutrient-rich lakes of the Boreal Plain (Mitchell and Prepas 1990), characterized by favorable light quality (Chambers and Prepas 1988), have high density macrophyte beds and extensive littoral zones. Therefore, littoral algae are expected to contribute substantially to photosynthesis and lake metabolism. Economic development on the Boreal Plain through forest harvesting, oil and gas exploration, and recreational activities has encouraged studies pertaining to the effects of such terrestrial disturbances on aquatic ecosystems. Knowledge of the contribution of littoral and pelagic algal photosynthesis will aid in refining models that focus on landscape-water quality interactions in relatively flat and nutrient-rich environments, such as the Boreal Plain. Since relatively little is known about the variables that influence littoral algae, initial research efforts need to examine relationships with biogeochemical variables.

The work described in this thesis was conducted in partnership with two large multidisciplinary projects: The Terrestrial and Riparian, Organisms, Lakes and Streams project was designed to study the impacts of forest harvesting on terrestrial and aquatic ecosystems in the aspen-dominated mixed-wood forest of Alberta, and Network of Centers of Excellence in Sustainable Forest Management was founded to provide student training in an environment involving numerous university-based disciplines, Canadian universities, and governments, industries and First Nations. The primary objective of my project was to determine the relative contributions of, and the variables influencing, littoral and pelagic algal photosynthesis in Boreal Plain lakes. Submersed macrophyte surface area was estimated in four lakes (Long Lake, SPH 20, 200, and 800, Figure 1.1) with a colorimetric method (Cattaneo and Carignan 1983), and species- and lake-specific

relationships with macrophyte biomass were determined (Chapter Two). Based on available macrophyte surface area, the contribution of epiphyton to littoral and whole-lake algal photosynthesis was compared in four lakes (SPH 20, 100, 200 and 800, Figure 1.1) with phytoplankton contributions (Chapter Three). Epiphyton were sampled on artificial substrata and rates of algal photosynthesis were estimated with the ^{14}C technique in the laboratory.

In Chapter Two, I tested the hypotheses that: 1) Macrophytes have more surface area per g of dry weight in lakes with relatively higher than lower water nutrient concentrations, and lower than higher light penetration, and 2) Macrophytes with dissected leaves provide more surface area per g dry weight than those with entire leaves.

In Chapter Three, I tested the hypotheses that: 1) Volumetric rates of littoral phytoplankton photosynthesis will exceed those in the pelagic in all study lakes, 2) In the littoral zone, phytoplankton photosynthesis will be related to TN, TP and phytoplankton biomass, while epiphyton photosynthesis will vary only with epiphyton biomass, and 3) The proportion of littoral surface area and contribution to whole-lake algal photosynthesis will be related.

1.3 References

Allen, H.L. & Ocevski, B.T. 1981. Comparative primary productivity of algal epiphytes on three species of macrophyte in the littoral zone of Lake Ohrid, Yugoslavia. *Holarctic Ecology* 4:155-160.

Brown, C.L. & Manny, B.A. 1985. Comparison of methods for measuring surface area of submersed aquatic macrophytes. *J. Freshwater Ecol.* 3: 61-68.

Burkholder, J-A.M. & Wetzel, R.G. 1990. Epiphytic alkaline phosphatase on natural and artificial plants in an oligotrophic lake: Re-evaluation of the role of macrophytes as a phosphorus source for epiphytes. *Limnol. Oceanogr.* 35: 736-747.

Cattaneo, A. & Carignan, R. 1983. A colorimetric method for measuring the surface area of aquatic plants. *Aquat. Bot.* 17: 291-294.

Cattaneo, A. & Kalff, J. 1978. Seasonal changes in the epiphyte community of natural and artificial macrophytes in Lake Memphremagog (Que. & Vt.). *Hydrobiologia* 60: 135-144.

Cattaneo, A. & Mousseau, B. 1995. Empirical analysis of the removal rates of periphyton by grazers. *Ocecologia* 103: 249-254.

Chambers, P.A. & Kalff, J. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. *Can. J. Fish. Aquat. Sci.* 42: 701-709.

Chambers, P.A. & Prepas, E.E. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. *Can. J. Fish. Aquat. Sci.* 45: 1010-1017.

Duarte, C. M. & Kalff, J. 1990. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. *Limnol. Oceanogr.* 31:1072-1080.

Eminson, D. & Moss, B. 1980. The composition and ecology of periphyton communities in freshwater. I. The influence of host type and external environment on community composition. *Br. Phycol. J.* 15: 429-446.

France, R.L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.* 40: 1310-1313.

Gerber, D.T., Ehlinger, T.J. & Les, D.H. 1994. An image analysis technique to determine the surface area and volume for dissected leaves of aquatic macrophytes. *Aquat. Bot.* 48: 175-182.

Gessner, M.O., Schieferstein, B., Muller, U., Barkmann, S. & Lenfers, U.A. 1996. A partial budget of primary organic carbon flows in the littoral zone of a hardwater lake. *Aquat. Bot.* 55:93-105.

Hansson, L-A. 1990. Quantifying the impact of periphytic algae on nutrient availability for phytoplankton. *Freshwater Biol.* 24: 265-273.

Harris, G.P. 1978. Photosynthesis, productivity and growth: The physiological ecology of phytoplankton. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 10: 1-171.

Harrison, P.G. & Durance, C.D. 1985. Reductions in photosynthetic carbon uptake in epiphytic diatoms by water-soluble extracts of leaves of *Zostera marina*. *Marine Biology* 90: 117-119.

James, W.F. & Barko, J.W. 1991. Estimation of phosphorus exchange between littoral and pelagic zones during nighttime convective circulation. *Limnol. Oceanogr.* 36: 179-187.

Jenkerson, C.G. & Hickman, M. 1983. The spatial and temporal distribution of an epiphytic algal community in a shallow prairie-parkland lake - Alberta, Canada. *Holarctic Ecology* 6: 41-58.

Jenkerson, C.G. & Hickman, M. 1986. Interrelationships among the epipelon, epiphyton and phytoplankton in a eutrophic lake. *Int. Revue Ges. Hydrobiol.* 71(4):557-79.

Jones, R.C. 1984. Application of a primary production model to epiphytic algae in a shallow, eutrophic lake. *Ecology* 65: 1895-1903.

Kairesalo, T. 1980. Comparison of in situ photosynthetic activity of epiphytic, epipelic and planktonic algal communities in an oligotrophic lake, southern Finland. *J. Phycol.* 16:57-62.

Meulemans, J.T. 1988. Seasonal changes in biomass and production of periphyton growing upon reed in Lake Maarsseveen I. *Arch. Hydrobiol.* 112:21-42.

Mitchell, & Prepas, E.E. 1990. Atlas of Alberta Lakes. University of Alberta Press, Edmonton, pp. 675.

Morin, A. & Cattaneo, A. 1992. Factors affecting sampling variability of freshwater periphyton and the power of periphyton studies. *Can. J. Fish. Aquat. Sci.* 49: 1695-1703.

Muller, U. 1995. Vertical zonation and production rates of epiphytic algae on *Phragmites australis*. *Freshwater Biol.* 34:69-80.

Phillips, G.L., Eminson, D. & Moss, B. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4:203-126.

Raspopov, I.M., Andronikova, I.N., Dotsenko, O.N., Kurashov, E.A., Letanskaya, G.I., Panov, V.E., Rychkova, M.A., Telesh, I.V., Tchernykh, O.A. & Vorontsov, F.F. 1996. Littoral zone of Lake Ladoga: ecological state evaluation. *Hydrobiologia* 322: 39-47.

Riber, H.H., Sorensen, J.P. & Schierup, H.-H. 1984. Primary productivity and biomass epiphytes on *Phragmites australis* in a eutrophic Danish lake. *Holarctic Ecology* 7:202-10.

Riber, H.H. & Wetzel, R.G. 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnol. Oceanogr.* 32:1181-94.

Schindler, D.W. 1978. Factors regulating production and standing crop in the world's freshwaters. *Limnol. Oceanogr.* 23: 478-486.

Sher-Kaul, S., Oertlie, B., Castella, E. & Lachavanne, J.-B. 1995. Relationship between biomass and surface area of six submerged aquatic plant species. *Aquat. Bot.* 51: 147-154.

Smith, V.H. 1979. Nutrient dependence of primary productivity in lakes. *Limnol. Oceanogr.* 24:1051-64.

Sondergaard, M. & Sand-Jensen, K. 1978. Total autotrophic production in oligotrophic, Lake Kalgaard, Denmark. *Verh. Internat. Verein. Limnol.* 20: 667-673.

Spence, D.H.N., Campbell, R.M. & Chrystal, J. 1973. Specific leaf areas and zonation of freshwater macrophytes. *J. Ecol.* 61: 317-328.

Watala, K.B. & C. Watala. 1994. A photometric technique for the measurement of plant surface area: the adsorption of Brilliant Blue dye on to plant surfaces. *Freshwater Biol.* 31: 175-181.

Wetzel, R.G. 1983a. Limnology, 2nd edition. Saunders College Publishing, Toronto, pp. 767.

Wetzel, R.G. 1983b. Attached algal-substrata interactions: fact or myth, and when and how? In Periphyton of Freshwater Ecosystems. Edited by R.G. Wetzel. DrW, Junk Publishers, Boston. pp.207-215.

Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. *Verh. Internat. Verein. Limnol.* 24:6-24.

Wetzel, R.G., Rich, P.H., Miller, M.C. & Allen, H.L. 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. *Mem. Ist. Ital. Idrobiol.* 29(Suppl.)185-243.

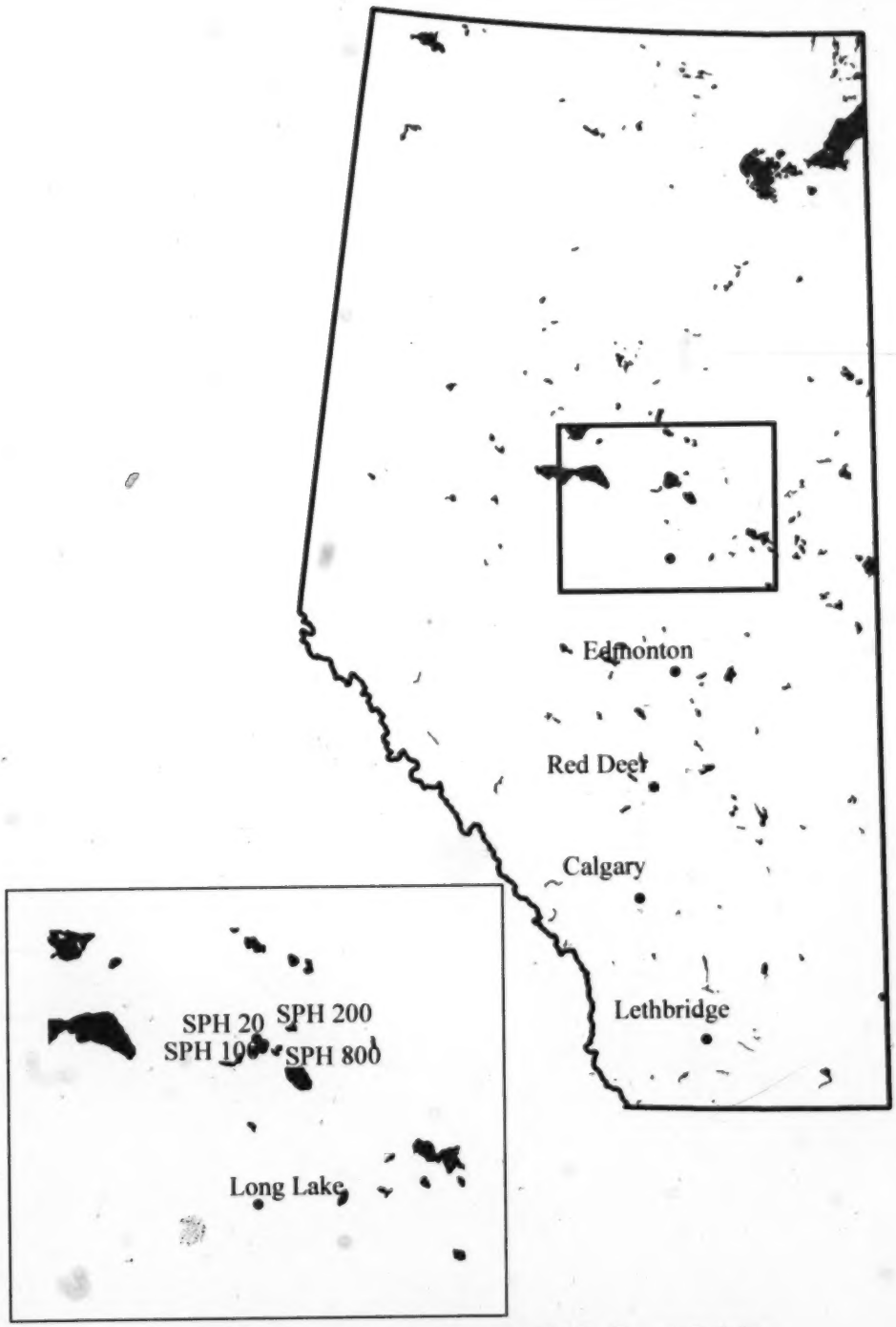


Figure 1.1: Map of Alberta with the five study lakes.

Chapter 2: Relationship between surface area and biomass of submersed macrophytes in lakes.

2.0 Introduction

Estimates of macrophyte surface area are critical to quantitative study of epiphytic organisms. However, current methods for estimation of macrophyte surface area are laborious involving colorimetric techniques (Cattaneo and Carignan 1983, Watala and Watala 1994), image analysis (Gerber et al. 1994) and physical measurements of leaf area (Spence et al. 1973, Brown and Manny 1985). Sher-Kaul et al. (1995) suggested that standard relationships between surface area and biomass would allow researchers to convert readily available estimates of macrophyte biomass into surface area available for epiphyton colonization.

However, general applicability of relationships between surface area and biomass assume consistency of patterns between lakes. However, consistency is highly unlikely since previous authors have noted variations in both macrophyte morphology (Spence and Dale 1978) and specific leaf area ($cm^2 \cdot g^{-1}$) with changes in water column depth (Clason 1953), light penetration (Spence et al. 1973), temperature (Johnson 1967), and substrate and water nutrient content (Siden-Hempstead and Killingback 1996). For example, *Nymphaeae odorata* had a larger leaf surface area in eutrophic as compared to oligotrophic ponds (Sinden-Hempstead and Killingback 1996). Leaf surface area can also increase with decreases in available light (Spence et al. 1973). Leaf dissection in *Ranunculus flabellaris* increased inversely with water temperature (Johnson 1967) while declining water levels produced shorter *Potamogeton lucens* leaves (Clason 1953). Variations in morphology and specific leaf area suggest that the relationship between macrophyte surface area and biomass may differ between lakes thereby limiting suitability for application across lakes.

Relationships between surface area and biomass may also be species-specific (Sher-Kaul et al. 1995, Nielsen and Sand-Jensen 1991) and depend on leaf morphology and the ratio of leaves to stems. Species-specific differences in dissected, fenestrate and entire leaf morphology would be expected to provide different amounts of surface area per g of dry weight. Despite these predictions, Sher-Kaul et al. (1995) noted that dissected leaf morphology did not necessarily result in larger surface area per unit of biomass. However, morphologically dependent metholodogy may have influenced the interpretation of results (Sher-Kaul et al. 1985). In addition, the relative proportion of leaves vs. stems may impact the surface area to biomass relationship since for most macrophyte species, leaves provide more surface area than stems (Sher-Kaul et al. 1995). To assess potential species-specific differences, comparison of the relationship between macrophyte surface area and biomass requires a single methodology.

Four lakes were chosen to maximize disparity in the variables thought to influence the relationship between macrophyte surface area and biomass, in particular, trophic classification (mesotrophic to hyper-eutrophic) and underwater light extinction. The following hypotheses were tested: 1) Macrophytes have more surface area per g of dry weight in lakes with relatively higher than lower water nutrient concentrations, and lower than higher light penetration, and 2) Macrophytes with dissected leaves provide more surface area per g dry weight than those with entire leaves.

2.1 Methods

2.1.1 Study site and sample collection

In late August 1999, six species of submersed macrophytes (Table 2.1) were randomly collected by a SCUBA diver at a depth of 1 m in four lakes on the Boreal Plain

(SPH 20, 200, 800 at 55°23'N, 113°40'W and Long Lake at 54°35'N, 113°39'W). Lakes varied from shallow to deep with mean depths of 2.2, 3.3, 4.6 and 9.4 m in SPH 800, 200, 20, and Long Lake, respectively. Macrophyte samples were returned to the laboratory in darkened coolers and sorted based on species identification. To dislodge epiphytes, macrophytes were shaken in a 4 L mason jar and rinsed until the water appeared clear. Samples of each macrophyte species were cut to obtain 15 individual macrophyte pieces ranging from 0.7 to 10 g wet weight. The 15 macrophyte pieces were chosen to represent the range of leaf and stem combinations that existed in the study lakes. The process was repeated in each lake for all submersed macrophyte species present.

2.1.2 Estimation of macrophyte surface area and dry weight

Macrophyte surface area was estimated colorimetrically (Cattaneo and Carignan 1983). Each macrophyte piece was dipped in a solution of 50% detergent (Purex Mountain Breeze) and 50% tap water dyed with blue fabric dye (Tintex Royal Blue #6 15.8 $g \cdot L^{-1}$). The sample was shaken 30 times and then submersed in a known volume of tap water (range 0.025 to 0.700 L). Color of the tap water was measured with a spectrophotometer (Spectronic 501 Milton Ray Company) at 597 nm. Spectrophotometric readings were then adjusted by multiplying by the volume of water used to rinse the macrophyte piece (dilution factor). The procedure was repeated three times for each macrophyte piece and the three adjusted spectrophotometric readings were averaged.

A standard curve was calculated to establish the relationship between color of the tap water and macrophyte surface area. Various leaves were selected and photocopied onto plain paper. Surface area was estimated with a planimeter and then doubled to

represent both sides of the leaf. Plant leaves were then rinsed in tap water and dipped in detergent/dye solution, shaken, and submersed in tap water as described above. Color of the resulting tap water was determined with a spectrophotometer. A standard curve was produced by plotting the relationship between the spectrophotometric readings and the measured surface area of each leaf ($r^2 = 0.97$, $P = 0.002$) and was then used to convert mean adjusted spectrophotometric readings from the macrophyte samples (above) into surface area.

Dry weight of the macrophyte samples was measured with a Mettler PE 36 (accuracy 0.005 g) after each piece was dried at 60°C to a constant weight. For Long Lake samples, duplicate macrophyte pieces with the same wet weight were used to determine the influence of the detergent/dye solution on dry weight. One piece was analyzed as above for surface area, while the other was dried and weighed without immersion in the detergent/dye solution.

2.1.3 Study lake physical, chemical and biological characteristics

Water chemistry, temperature, and lake-water levels were measured monthly in SPH 20, 200, and 800 in June, July, August and September of 1998 (E.E. Prepas, unpublished data). Water samples were collected from the euphotic zone with an integrated sampler near the point of maximum depth of the lake. The euphotic zone was defined as the depth of penetration of 1% of the surface irradiance as measured at 1 m intervals with a LiCor quantum sensor (Model LI-192SA). Temperature was measured with a YSI model 57 DO/temperature meter at the surface and at 1 m depth and averaged. Samples for total dissolved phosphorus (TDP) were filtered within 24 h, through pre-rinsed (with doubled distilled water) 0.45 µm Millipore (HAWP) filters. Samples for

TDP and total phosphorus (TP) were digested by Menzel and Corwin's (1965) potassium persulfate method and analyzed following a modified molybdenum blue colorimetric method (Prepas and Rigler 1982). Samples for ammonia - N (NH_4^+) were analyzed on an autoanalyser following Solozano's (1969) phenolhypochlorite method. Monthly measurements of water chemistry and temperature were averaged to produce mean summer estimates (Table 2.2). Maximum depth of each lake was measured once every two weeks throughout the spring and summer of 1997 to 1999 for assessment of water level fluctuations before and during the study.

Triplicate samples for phytoplankton biomass were collected with an integrated sampler to a depth of 3 m in SPH 20 and 200, and to a depth of 2 m in SPH 800 near the point of maximum depth. Phytoplankton samples were collected onto Whatman GF/C filters and were then frozen for a period of up to 4 weeks before analysis of chlorophyll *a* (chl*a*) concentration with 95% hot ethanol (Sartory and Grobbelaar 1984).

Measurements of PAR throughout the water column were made with a LiCor spherical quantum sensor (Model LI-193SA) at 12 littoral stations in SPH 20, 200 and 800 (0.75 or 1.5 m depth). Vertical extinction coefficient (E_{PAR}) was calculated between the surface and 0.5 m depth (Weztel 1983) and averaged for all stations to provide a lake-wide estimate. Monthly E_{PAR} was averaged to produce mean summer estimates (Table 2.2).

Long Lake water chemistry and phytoplankton biomass data for 1986 were obtained from the Atlas of Alberta Lakes (Mitchell and Prepas 1990), while E_{PAR} values for the same year were obtained from Chambers and Prepas (1990). Water chemistry, phytoplankton biomass and light extinction in mesotrophic Long Lake are presumed to

have little year-to-year variation as shown in neighboring mesotrophic Narrow Lake (R. Zurawell, unpublished, Mitchell and Prepas 1990,).

2.1.4 Statistical analyses

Dry weight of Long Lake macrophyte samples dipped and not dipped in detergent were compared with either a paired *t*-test (normally distributed data) or a Wilcoxon Signed-Rank test (nonparametric data). Linear regressions of surface area (dependent variable) on biomass (independent variable) were compared between species and lakes with an Analysis of Covariance (Zar 1974, ANCOVA JMP IN® Software - SAS Institute 1996). Although residuals for all linear regressions were normal, some heterogeneous variance was present. Since sample sizes were equal or nearly equal, it was assumed that the analysis was robust enough to operate well with heteroscedasticity (Zar 1974). Power analysis of the ANCOVA was conducted to determine probability of a type II error (β), power ($1-\beta$). The sample size required to detect differences or the number of observations needed to drive down the variance of the estimates enough to achieve a significant result with the given values of alpha, sigma, and delta (the significance level, the standard deviation of the error, and the effect size, respectively) was also estimated (SAS Institute 1996). Newman-Keuls multiple range test was used for multiple comparisons (Zar 1974). The surface area of 1 g dry weight of each macrophyte in each lake was predicted with linear regression and compared between species with individual lakes as replicates with one-way analysis of variance (ANOVA, SAS Institute 1996). Tukey-Kramer HSD was used for multiple comparisons. *Utricularia vulgaris* and *Potamogeton pusillus* were omitted from the statistical analysis as they was found only in

Long Lake and SPH 800, respectively. Differences were considered significant if $P<0.05$.

2.2 Results

A gradient of NH_4^+ and TP concentration and light extinction coefficients ranging up to 23, 6 and 5 fold, respectively, was found across the study lakes. Mean NH_4^+ concentration in SPH 200 was 42, 17 and 12 times higher than in Long Lake, SPH 20 and 800, respectively (Table 2.2). High NH_4^+ concentrations in SPH 200 were attributed to decomposition associated with 3.5 m fluctuations in water level due in part to beaver activity and large fluctuations in runoff (Prepas et al. in prep). Mean TP concentration in SPH 800 was about 6, 3 and 2 times higher than in Long Lake, SPH 200 and 20, respectively. Light penetrated deeper in Long Lake where mean E_{PAR} was between 2.5 and 5 times lower than in the SPH lakes and E_{PAR} in SPH 800 was almost 2 times higher than in SPH 20 and 200 (Table 2.2). Based on maximum phytoplankton chl*a* concentration, Long Lake and SPH 200 were mesotrophic, and SPH 20 was eutrophic and SPH 800 was hypereutrophic (OECD 1982). The study lakes provide a range of chemical, physical and biological characteristics for comparing the relationship between macrophyte surface area and biomass.

Comparison of the dry weight of samples dipped, and not dipped, in detergent/dye solution showed either no detectable difference or a lower weight for dipped samples (Table 2.3). Therefore, absorption of residual detergent/dye solution did not appear to result in an increase in the dry weight of dipped macrophytes. However, shaking samples to remove excess detergent/dye may have dislodged pieces of macrophyte into the solution resulting in a lower weight of dipped samples. Comparison of the dry weight of

samples dipped and not dipped may not have provided quantitative assessment of the tendency of macrophytes to absorb the detergent/dye solution.

With the exception of *P. pusillus*, macrophyte surface area was positively related to biomass (Table 2.4, and Figures 2.1, 2.2 and 2.3). *P. pusillus* was therefore excluded from any subsequent analysis. For the remaining macrophyte species, surface area can be predicted from biomass however, the proportion of variance in surface area explained by biomass (r^2) varied greatly between 0.34 and 0.96. While the relationship between biomass and surface area was consistently high between lakes for *Ceratophyllum demersum*, the relationship was highly variable for *Potamogeton richardsonii*, *Potamogeton zosterformis* and *Myriophyllum exalbescens*. The proportion of variance in surface area explained by biomass was independent of leaf morphology, since dissected *C. demersum* and entire *P. richardsonii* had higher r^2 values than dissected *M. exalbescens* and entire *P. zosteriformis*.

Comparison of the relationship between macrophyte surface area and biomass, for each species, indicated differences (Table 2.5). However, multiple comparison analyses showed no consistent groupings, or patterns that could relate the different relationships to macrophyte leaf morphology. However, when quantity of macrophyte surface area per g of dry weight was compared between species, groupings based on leaf morphology were apparent. Surface area per g dry weight was higher for the dissected leaf macrophyte *U. vulgaris* (2030 $cm^2 \cdot g^{-1}$) compared to dissected leaf *C. demersum* and *M. exalbescens* (478 and 429 $cm^2 \cdot g^{-1}$, respectively). The higher surface area provided by *U. vulgaris* as may be attributable to the numerous bladders present on *U. vulgaris*. Although both

P. richardsonii (716 $cm^2 \cdot g^{-1}$) and *P. zosteriformis* (213 $cm^2 \cdot g^{-1}$) have entire leaves, the thin, long, linear morphology of *P. zosteriformis* may have accounted for its lower surface area as compared to *P. richardsonii* with wider, oval leaf morphology.

With the exception of *C. demersum*, the relationship between surface area and biomass for each macrophyte species was not detectably different between study lakes. Although, the surface area to biomass relationship was indistinguishable between lakes for *P. richardsonii*, *P. zosteriformis*, and M. *exalbescens* (Table 2.6), low power (power = 0.5, 0.44 and 0.05 for *P. richardsonii*, *P. zosteriformis*, and M. *exalbescens*, respectively) may have contributed to the lack of detectable differences. Repeat analysis with increased sample size of 30 replicates per macrophyte species, as compared to the 15 used in this study, would enhance the power of the analysis and could allow detection of potential differences. Differences were detected for *C. demersum* which provided less surface area per unit of biomass in SPH 200 as compared to SPH 20, 800 and Long Lake. Detection of differences in the relationship between *C. demersum* surface area and biomass may be related to the high power associated with this analysis (power = 0.96). Despite a range of nutrient concentrations and light extinction coefficients, many of the species-specific relationships between macrophyte surface area and biomass were not detectably different between lakes.

2.3 Discussion

Except for *P. pusillus*, the strong positive relationship observed between surface area and biomass for all macrophyte species suggests that colorimetric/dry weight is a reliable method for determining surface area. Since *P. pusillus* was found only in SPH 800, it was difficult to determine if the poor relationship was an isolated situation or if the

methodology was poorly suited to the small, threadlike leaves. The application of the colorimetric/dry weight methodology to macrophytes with threadlike leaf morphology merits further consideration.

The relationship between macrophyte surface area and biomass is highly species-specific yet differences do not appear to be related to basic categories of dissected and entire leaf morphology. When dissected leaf macrophytes are examined based on presence or absence of bladders, bladder-absent *C. demersum* and *M. exalbescens* had lower surface area than *U. vulgaris* with its numerous bladders. Although entire leaf *P. zosterformis* had lower surface area than entire leaf *P. richardsonii*, the difference can be attributed to long, linear vs. wide, oval leaf morphology. My results agree with those of Sher-Kaul et al. (1996) who suggested that the relationship between surface area and biomass was not dependent on leaf morphology. However, grouping of morphologically similar species (i.e. *C. demersum* and *M. spicatum*) could be considered when converting macrophyte biomass to surface area.

Contrary to my hypothesis, relationships between species-specific macrophyte biomass and surface area were remarkably similar in the four study lakes. Despite mean summer E_{PAR}, NH_4^+ and TP concentrations ranging between 0.7 to 3.3 m^{-1}, 4 to 168 $\mu g \cdot L^{-1}$, and 13 to 78 $\mu g \cdot L^{-1}$, respectively, the relationship between surface area and biomass for *P. richardsonii*, *P. zosteriformis* and *M. exalbescens* were not detectably different. However, small sample sizes may have reduced my ability to detect differences in the species-specific surface area to biomass relationship and therefore future research should focus on larger sample sizes of about 30 replicates per macrophyte.

In contrast, *C. demersum* plants in SPH 200 provided less surface area per unit of biomass as compared to the other lakes. Since stems provided less surface area per unit of biomass than leaves on a morphologically similar plant, *Myriophyllum spicatum* (Sher-Kaul et al. 1995), the proportion of leaves vs. stems may be smaller in SPH 200 as compared to the other lakes. Dissected leaves may also show differences in the degree of subdivision, length and thickness of segments under different conditions such as water level fluctuations (Sculthorpe 1985). Water level in SPH 200 fluctuated over 3 m between 1997 and 1999 although lake levels were relatively high during sampling. *C. demersum* has a high tolerance for variable water level (Barrat-Segretain et al. 1999) and therefore plants in SPH 200 may have represented those adapted to towards survivorship consisting of more buds and fragments and fewer whole plants than those in the other lakes. *C. demersum*, a submergent yet free-floating macrophyte, may also have whitish thread-like segments that penetrate the substrate aiding in adsorption and anchorage (Sculthorpe 1985). Presence of more rhizoid shoots on *C. demersum* plants in SPH 200 may have reduced the surface area relative to dry weight. Difference in the surface area provided by *C. demersum* may also be related to the large difference (up to 42 times) in NH_4^+ concentration in SPH 200 compared to SPH 20, 800 and Long Lake. Previous study of *Nymphaea odorata* by Sinden-Hempstead and Killingbeck (1996) noted higher leaf surface area in eutrophic as compared to oligotrophic ponds. In contrast, my results suggest smaller leaf surface area per unit of biomass at higher NH_4^+ concentration. Therefore, fluctuating water level, presence/absence of rhizoids and high NH_4^+ concentration may have altered the relationship between *C. demersum* surface area and biomass in SPH 200 as compared to the other study lakes.

Finally, do relationships between macrophyte surface area and biomass have general applicability between lakes? Comparison of the results of this study with those for Lake Geneva (Sher-Kaul et al. 1995) suggest that while some relationships between surface area and biomass are similar, others are dramatically different. For example, mean surface area provided by 1 g dry weight of *P. richardsonii* (716 cm^2) in this study is similar to that provided by morphologically similar *P. perfoliatus* (762 cm^2) in Lake Geneva (Sher-Kaul et al. 1995). In contrast, *M. spicatum* from Lake Geneva provided more than two times the mean surface area per g of dry weight of morphologically comparable *M. exalbescens* in our study lakes. Although this study provided only one example of detectable differences in the surface area to biomass relationship between lakes, low sample size was a factor as indicated by the low power. In the one comparison associated with high power, differences were detected. Therefore, based on comparisons with Lake Geneva and between lakes on the Boreal Plain, the relationship between macrophyte surface area and biomass differs between lakes. However, further research with larger sample sizes, addressing in particular changes in water level fluctuations and NH_4^+ concentration, is required to provide more insight into where and why such differences occur.

2.4 References

Barrat-Segretain, M.-H., Henry, C.P. and Bornette, G., 1999. Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. Arch. Hydrobiol. 145, 111-127.

Brown, C.L. and Manny, B.A., 1985. Comparison of methods for measuring surface area of submersed aquatic macrophytes. J. Freshwater Ecol. 3, 61-68.

Cattaneo, A. and Carignan, R., 1983. A colorimetric method for measuring the surface area of aquatic plants. Aquat. Bot. 17, 291-294.

Clason, E.W., 1953. Notes on the Potamogetones of the Zuidlaren Lake and its adjacent waters. Acta Bot. Neerl. 1, 489-496.

Chambers, P.A. and Prepas, E.E., 1990. Competition and coexistence in submerged aquatic plant communities: the effects of species interactions versus abiotic factors. Freshwater Biol. 23, 541-550.

Gerber, D.T., Ehlinger, T.J. and Les, D.H., 1994. An image analysis technique to determine the surface area and volume for dissected leaves of aquatic macrophytes. Aquat. Bot. 48, 175-182.

Johnson, M.P., 1967. Temperature dependent leaf morphogenesis in *Ranunculus flabellaris*. Nature 214, 1354-1355.

Menzel, D.W. and Corwin, N., 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10, 280-282.

Mitchell, and Prepas, E.E., 1990. Atlas of Alberta Lakes. University of Alberta Press, Edmonton, pp. 675.

Nielsen, S.L. and Sand-Jensen, K., 1991. Variation in growth rates of submerged rooted macrophytes. Aquat. Bot. 39,109-120.

OECD, 1982. Eutrophication of waters. Organization for Economic Co-operation and Development, Paris, pp. 154.

Prepas, E.E. and Rigler, F.H., 1982. Improvements in quantifying the phosphorus concentration in lake water. Can. J. Fish. Aquat. Sci. 39, 822-829

Sartory, D.P. and Grobbelaar, J.U., 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114, 177-87.

SAS Institute, 1996. JMP® Start Statistics: A Guide to Statistical and Data Analysis Using JMP® and JMP IN® Software. Duxbury Press, Toronto.

Sculthorpe, C.D. 1985. The Biology of Aquatic Vascular Plants (Reprint of 1967 edition). Edward Arnold Ltd, London, pp. 610.

Sher-Kaul, S., Oertlie, B., Castella, E. and Lachavanne, J.-B., 1995. Relationship between biomass and surface area of six submerged aquatic plant species. Aquat. Bot. 51, 147-154.

Sinden-Hempstead, M. and Killingback, K.T., 1996. Influences of water depth and substrate nitrogen on leaf surface area and maximum bed extension in *Nymphaea odorata*. Aquat. Bot. 53, 151-162.

Solorzano, L., 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnol. Oceanogr. 14: 799-801

Spence, D.H.N. and Dale, H.M., 1978. Variations in the shallow water form of *Potamogeton richardsonii* induced by some environmental factors. Freshwater Biol. 8, 251-268.

Spence, D.H.N., Campbell, R.M. and Chrystal, J., 1973. Specific leaf areas and zonation of freshwater macrophytes. J. Ecol. 61, 317-328.

Watala, K.B. and C. Watala., 1994. A photometric technique for the measurement of plant surface area: the adsorption of Brilliant Blue dye on to plant surfaces. Freshwater Biol. 31, 175-181.

Wetzel, R.G., 1983. Limnology, 2nd edition. Saunders College Publishing, Toronto.

Zar, J.H., 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Table 2.1: Morphological characteristics and presence/absence of the six macrophyte species in the study lakes.

Macrophyte Species	Leaf morphology	Leaf shape	Long Lake	SPH 20	SPH 200	SPH 800
Potamogeton zosteriformis Fern.	Entire	linear	X		X	X
Potamogeton richardsonii Rydb.	Entire	Oval to linear	X	X		X
Myriophyllum exalbescens Fern.	Dissected	Whorl	X	X	X	
Ceratophyllum demersum L.	Dissected	Whorl	X	X	X	X
Utricularia vulgaris L.	Dissected	Bladder	X			
Potamogeton pusillus L.	Entire	Threadlike				X

Table 2.2: Mean summer general chemical, biological and physical characteristics of the study lakes.

	SPH 20	SPH 200	SPH 800	Long Lake
NH_4^+ ($\mu g \cdot L^{-1}$)	14	168	9.8	4[b]
TP ($\mu g \cdot L^{-1}$)	24	36	78	13[b]
Phytoplankton chl*a* ($\mu g \cdot L^{-1}$)	5.1[a]	7.7[a]	29[a]	3.9[b]
E_{PAR}	1.9[a]	1.4[a]	3.1[a]	0.7[c]
Water temperature (°C)	19.8	19.8	19.6	na

Sources: E.E. Prepas, unpublished data from 1998 and,
a: This study from 1998
b: Mitchell and Prepas 1990 from 1986
c: Chambers and Prepas 1990 from 1986

Table 2.3: Comparison of the dry weight of Long Lake macrophyte species dipped in dye and those without immersion in dye (P = probability).

	P value	n	Dipped weight (g)	Non-dipped weight (g)	Test
C. demersum	0.09	15	0.31	0.34	Paired-*t*
M. exalbescens	0.003	15	0.13	0.17	Wilcoxon signed rank
P. richardsonii	0.04	15	0.22	0.25	Paired-*t*
P. zosteriformis	0.07	15	0.43	0.47	Wilicoxon signed rank

Table 2.4: Regression parameters for the relationship between macrophyte surface area (dependent variable cm^2) and biomass (independent variable g dry weight) for each species in the study lakes (± SE).

Species	Lake	*n*	α	β	r^2	*P*
C. demersum	20	14	31 ± 8.0	595 ± 47	0.93	<0.0001
C. demersum	200	13	80 ± 12	227 ± 33	0.81	<0.0001
C. demersum	800	12	45 ± 12	474 ± 46	0.91	<0.0001
C. demersum	Long Lake	15	63 ± 20	399 ± 54	0.81	<0.0001
M. exalbescens	20	15	1.7 ± 7.0	528 ± 30	0.96	<0.0001
M. exalbescens	200	15	31 ± 28	464 ± 114	0.56	0.001
M. exalbescens	Long Lake	14	44 ± 12	219 ± 89	0.34	0.03
P. zosteriformis	200	13	49 ± 15	226 ± 50	0.65	0.0009
P. zosteriformis	800	15	71 ± 8	124 ± 32	0.54	0.002
P. zosteriformis	Long Lake	15	58 ± 9	112 ± 16	0.79	<0.0001
P. richardsonii	20	14	34 ± 12	704 ± 126	0.72	0.0001
P. richardsonii	800	15	25 ± 8	665 ± 82	0.84	<0.0001
P. richardsonii	Long Lake	14	60 ± 31	659 ± 128	0.69	0.0002
U. vulgaris	Long Lake	15	-19 ± 40	2048 ± 317	0.76	<0.0001
P. pusillus	800	14	33 ± 1.4	66 ± 49	0.13	0.20

Note: α = slope of the equation; β = intercept

Table 2.5: Probability values from an ANCOVA comparing both the slope and intercept of the relationship between macrophyte surface area (dependent variable) and biomass (independent variable) between species (independent variable).

	Slope	Intercept	*n*
Long Lake	<0.0001	-	73
SPH 20	0.2324	0.0136	43
SPH 200	0.0442	-	41
SPH 800	<0.0001	-	42

Table 2.6: Probability values from an ANCOVA comparing both the slope and intercept of the relationship between macrophyte surface area (dependent variable) and biomass (independent variable) between lakes (independent variable) for each macrophyte species.

	Slope	Intercept	*n*
C. demersum	0.001	-	54
P. richardsonii	0.98	0.44	43
P. zosteriformis	0.12	0.49	43
M. exalbescens	0.08	0.13	44

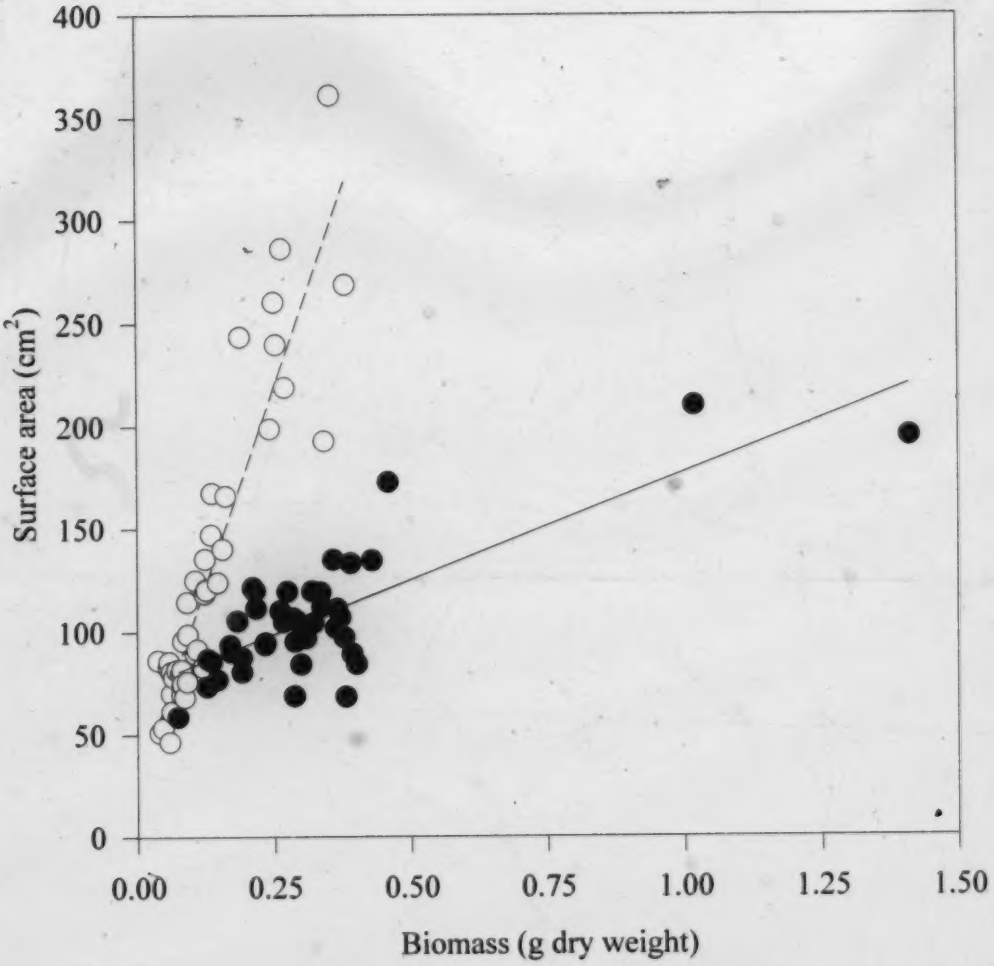


Figure 2.1: *P. richardsonii* and *P. zosteriformis* surface area related to biomass and least squares regression line.

○ *P. richardsonii*

– – – $y = 26x + 769$, $r^2 = 0.85$, $P < 0.001$

● *P. zosteriformis*

—— $y = 73x + 104$, $r^2 = 0.61$, $P < 0.0001$

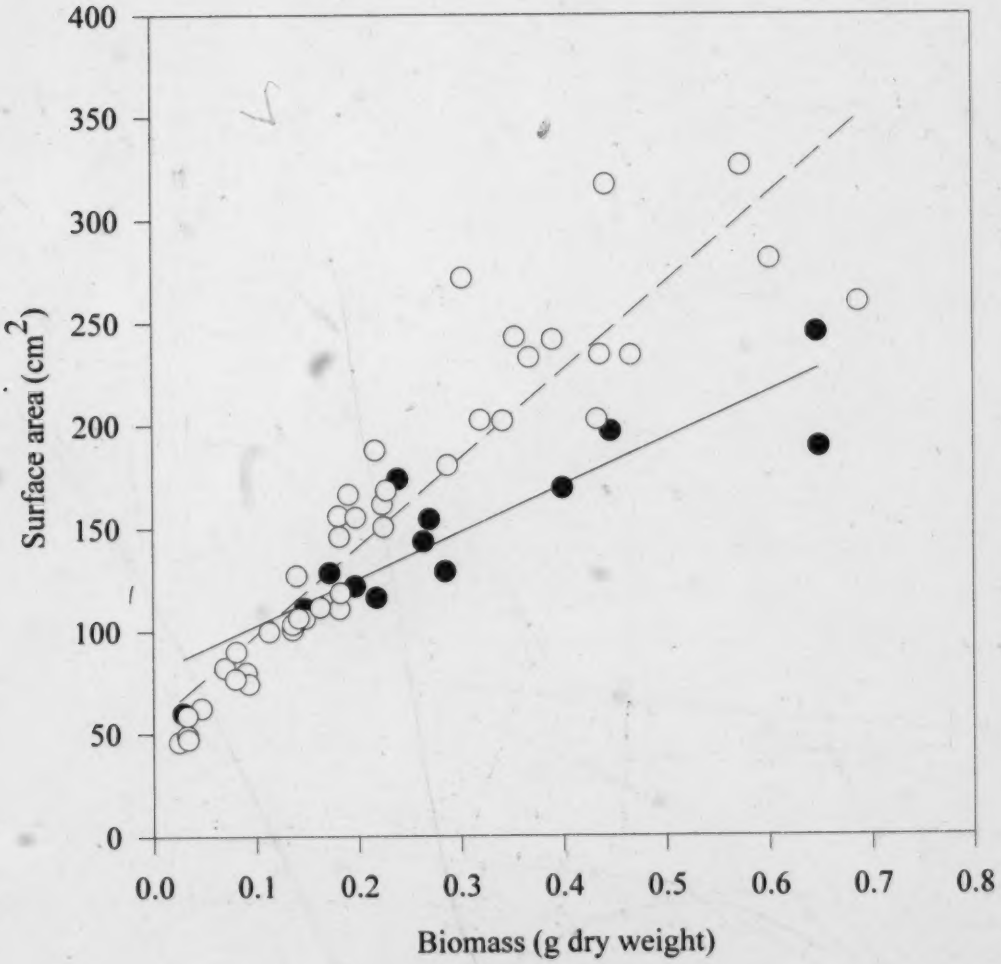


Figure 2.2: *C. demersum* surface area related to biomass and least squares regression line.

● SPH 200

—— $y = 80x + 227$, $r^2 = 0.81$, $P < 0.0001$

○ SPH 20, SPH 800 and Long Lake

– – $y = 55x + 428$, $r^2 = 0.86$, $P < 0.0001$

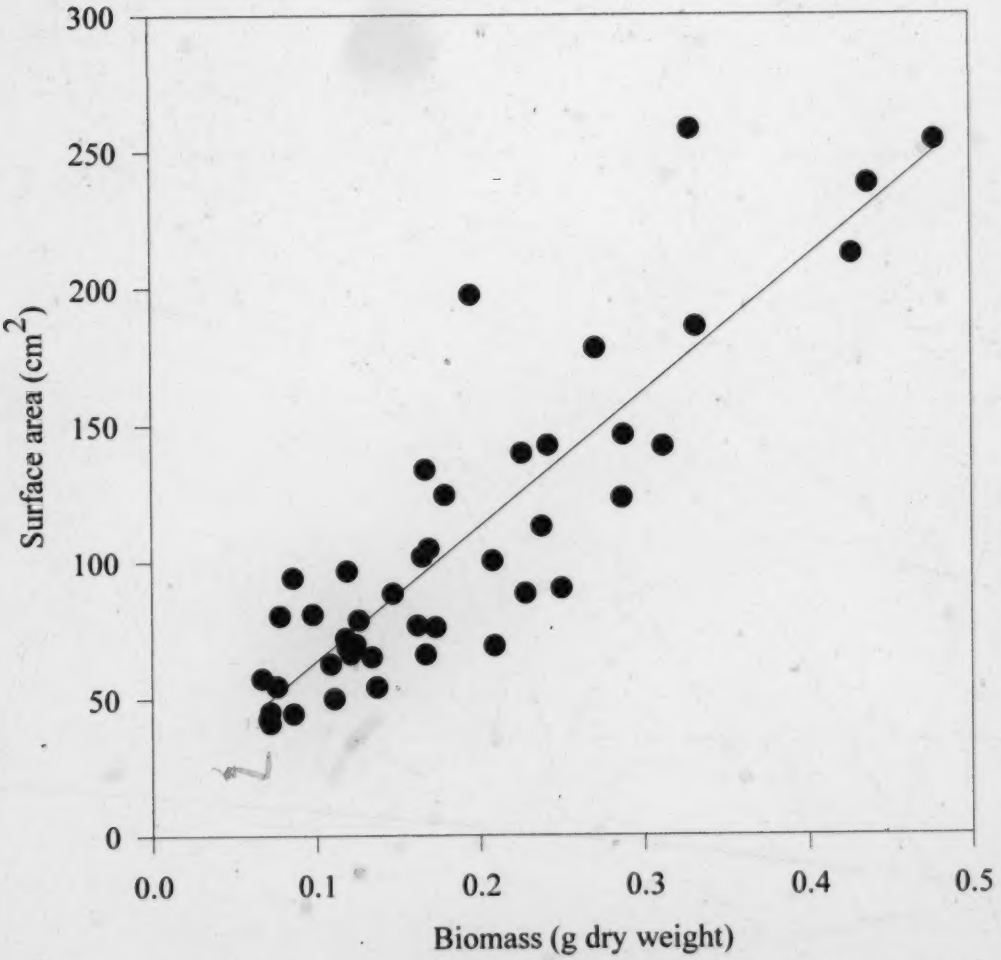


Figure 2.3: *M. exalbescens* surface area related to biomass and least square regression line.

● *M. exalbescens*

——— $y = 14x + 493$, $r^2 = 0.77$, $P < 0.0001$

Chapter Three: Relative contribution of littoral and pelagic algae to whole-lake algal photosynthesis in eutrophic lakes.

3.0 Introduction

Previous studies investigating algal photosynthesis in lakes have focused on the pelagic zone, despite the possibility that a major portion of whole-lake photosynthesis may occur in the littoral (Wetzel 1993). Whereas phytoplankton inhabit both zones, epiphyton (algae attached to macrophytes) are present only in the littoral zone, the interface zone between the highest seasonal water level and the maximum depth of macrophyte colonization (Wetzel 1983a). Therefore, while pelagic algal photosynthesis consists only of free-floating algae, littoral algal photosynthesis can occur as both free-floating and attached algae. Most studies on algal photosynthesis in littoral and pelagic zones have focused on the latter and it is unclear where littoral contributions predominate.

Previous research suggests that the contribution of littoral algae to whole-lake algal photosynthesis may depend on lake morphometry, and both macrophyte density and distribution (Kairesalo 1980, Jenkerson and Hickman 1986). In shallow lakes with high macrophyte density, algal photosynthesis in the littoral zone may exceed that in the pelagic. Yet the literature suggests that relatively higher pelagic algal photosynthesis persists regardless of lake depth or trophic classification (Sondergaard and Sand-Jensen 1978, Allen and Ocevski 1981, Kairesalo 1980, Jones 1984, Gessner et al. 1996). However, surface area of the littoral zone, relative to the pelagic, is expected to be related to lake morphometry and macrophyte distribution (Wetzel 1983a). Although contribution to whole-lake algal photosynthesis, and relative size, of the littoral and pelagic zones are linked, the relationship has yet to be quantified.

Measurements of phytoplankton photosynthesis are required in both zones to determine if pelagic rates can be extrapolated to the littoral. Only two studies in the literature provide pelagic and littoral rates of phytoplankton photosynthesis (Allen and Ocevski 1981, Gessner et al. 1996). In both cases, the pelagic relative to the littoral zone had higher areal rates of photosynthesis although the greater depth of the former sample may have contributed to the difference. However, littoral phytoplankton biomass may exceed that of the pelagic zone and/or water temperature may be higher within macrophyte beds. Yet, pelagic phytoplankton photosynthesis may be enhanced relative to the littoral due to the absence of competition for light and nutrients from epiphyton and macrophytes (Phillips et al. 1978, Wetzel 1983a, Hansson 1990). Clearly, littoral and pelagic rates ($m^3 \cdot d^{-1}$) of phytoplankton photosynthesis could differ dramatically making assessment of both essential to whole-lake models.

Total phosphorus (TP), total nitrogen (TN) and phytoplankton biomass correlate with rates of pelagic phytoplankton photosynthesis in a wide range of North American lakes (Schindler 1978, Smith 1979). However, rates of epiphyton photosynthesis may not correlate with nutrient concentrations and light extinction as the chemical and physical conditions within the epiphytic mat can differ from the immediate surroundings (Riber and Wetzel 1987). As a result, studies of epiphyton photosynthetic rates have focused primarily on correlation with biomass (Kairesalo 1980, Jenkerson and Hickman 1983, Jones 1984, Muller 1995). Conditions within the epiphytic mat may reflect higher nutrient competition and reduced light penetration due to high cell densities (Kairesalo 1980, Riber et al. 1984, Meulemans 1988, Muller 1995) as compared to free-floating algae. Therefore, rates of littoral phytoplankton photosynthesis are expected to correlate

with seasonal fluctuations in TP, TN and phytoplankton biomass, whereas epiphyton photosynthesis and biomass may only be related to each other.

I expect littoral algal photosynthesis to exceed that of the pelagic in shallow lakes with extensive and dense macrophyte beds. Thus, the shallow, nutrient- and light-rich lakes of the Boreal Plain are ideal systems in which to evaluate the contribution of the littoral zone to whole-lake algal photosynthesis. I selected lakes with a wide range of littoral to total surface area (between 24 and 78%) to test the following hypotheses: 1) Volumetric rates of littoral phytoplankton photosynthesis will exceed those in the pelagic in all study lakes, 2) In the littoral zone, phytoplankton photosynthesis will be related to TN, TP and phytoplankton biomass, while epiphyton photosynthesis will vary only with epiphyton biomass, and 3) The proportion of littoral surface area and contribution to whole-lake algal photosynthesis will be related.

3.1 Methods

3.1.1 Study sites

The study was conducted in four relatively small, shallow and remote lakes located on the Boreal Plain in aspen-dominated watersheds (55°23'N, 113°40'W) (Table 3.1, Prepas et al. 2000). Activity within the area consisted of oil and gas exploration, recent forest harvesting and recreational activity (hunting and fishing). Lakes were named by 'Terrestrial and Riparian, Organisms, Lakes and Streams' (TROLS) according to region (SPH = near South Pelican Hills) and planned buffer width between the lake and harvested blocks (SPH 20 scheduled to maintain a 20 m buffer).

3.1.2 Sampling

Lakes were sampled monthly from June to September 1998. For littoral sampling, three transects were selected in each lake with a station on each transect at 0.75 and 1.5 m depth (nearshore and farshore, respectively). Three pelagic stations were selected near the point of maximum depth of each lake. In all but one instance (SPH 20 in July between 0900 and 1300 h), littoral and pelagic stations were sampled between 730 and 1100 h. At each station, measurements of photosynthetically active radiation (PAR) were made at 0.25 m intervals from the surface to about 0.2 m above the sediment with a LiCor spherical quantum sensor (Model LI-193SA). Vertical extinction coefficient (E_{PAR}) was calculated between the surface and 0.5 m depth (Wetzel 1983a). At each littoral and pelagic station, water samples were collected with an integrated sampler from the surface to a depth of 0.55 and 1.3 m at nearshore and farshore stations, respectively, and to a depth of 2 m and 3 m at pelagic stations in SPH 100 and 800, and SPH 20 and 200, respectively. Water samples were placed in darkened Naglene bottles (polyethylene) and transported on ice in a cooler to the laboratory. Epiphyton were sampled with artificial substrata at each nearshore and farshore littoral station. Artificial substrata consisted of Nitex fabric stretched over Plexiglas rings and were first placed in the lakes in May 1999. Substrata were hung for 28 d from a metal bar suspended by a float and anchored on the sediment with a brick (Figure 3.1). To avoid the influence of surface waves, the maximum depth of which was calculated based on effective fetch (Wetzel 1983a), substrata were suspended at 0.5 m below the water surface. To sample epiphyton, Nitex fabric was removed from the Plexiglas ring with tweezers, folded in

quarters and placed in a plastic Petri dish. These dishes were wrapped in aluminum foil and transported to the laboratory on ice in a cooler for analysis within 1 h.

3.1.3 Chemical analyses

After storage at 4°C for 6 h, water samples for total and dissolved organic carbon (TC and DOC), and total dissolved nitrogen (TDN) analyses were filtered through 1.2 µm Whatman GF/C filters while those for total dissolved phosphorus (TDP) and nitrate-nitrite-N ($NO_3^-+NO_2^-$) were filtered through pre-rinsed (with double distilled water) 0.45 µm Millipore (HAWP) filters. Water samples for TP and TDP analyses were oxidized immediately with potassium persulfate, refrigerated at 4°C, and then within 14 d, digested (Menzel and Corwin 1965) and analyzed following a modified molybdebum blue colorimetric procedure (Prepas and Rigler 1982). Particulate phosphorus (PP) was estimated as TP minus TDP. Samples for ammonium- N (NH_4^+) and $NO_3^-+NO_2^-$ were analyzed within 24 h with an autoanalyzer following the phenolhypochlorite method of Solorzano (1969) and the cadmium-copper reduction method of Stainton et al. (1977), respectively. Dissolved inorganic nitrogen (DIN) was estimated as the sum of the NH_4^+ and $NO_3^-+NO_2^-$ concentrations. Total dissolved nitrogen (TDN) was estimated with an autoanalyzer after photocombustion in a UV digester with the method of Stainton et al. (1977). Total carbon (TC) and dissolved organic carbon (DOC) were estimated with the combustion infrared method of Greenberg et al. (1992) on a programmable carbon analyzer (Ionics model 1505) after samples were stored at 4°C for between two to five months. Dissolved inorganic carbon (DIC) was estimated as TC minus DOC. Soluble reactive silicon (Si) was estimated within 14 d with the molybdate method of Stainton et al. (1977).

3.1.4 Algal analysis

Phytoplankton and epiphyton samples were analyzed for biomass and photosynthetic rate in the laboratory. Epiphyton analyses were performed directly on the Nitex fabric. Pelagic and littoral phytoplankton analyses were performed on the pelagic and littoral water samples, respectively. Although the term "phytoplankton" is used to describe the littoral free-floating samples, they likely consist of both true planktonic species and algae that have become detached from substrata (macrophytes and sediments). For analysis of epiphyton biomass, one, 1 cm^2 section was cut from three different circles of Nitex fabric. For analysis of phytoplankton biomass, three replicate water samples were collected onto Whatman GF/C filters. Both the Nitex squares (epiphyton) and the filters (phytoplankton) were frozen for a period of up to 4 weeks before analysis of biomass (as chl*a*) and phaeopigment (pheo) concentrations with 95% hot ethanol extraction and acidification (Sartory and Grobbelaar 1984).

Rates of epiphyton and phytoplankton photosynthesis were estimated by measuring uptake of ^{14}C in the laboratory over a range of irradiance. Five ranges of irradiance (high 715 to 1523, medium-high 390 to 770, medium 187 to 371, medium-low 88 to 233 and low 11 to 43 $\mu mole \cdot m^{-2} \cdot s^{-1}$) were produced from two high pressure sodium vapor lamps (Day-Brite Micro Flood) in a water filled incubator (aluminum with one Plexiglas side - 1.2 x 0.7 x 0.2 m). Water temperature of the top 1 m of the pelagic was maintained in the incubator with a cooling and heating, circulating pump (Haake). For analysis of epiphyton photosynthetic rate, six circles of Nitex fabric from each littoral station were cut into three, 1 cm^2 sections. Each 1 cm^2 section was placed into one of 15 clear, or 3 darkened, test tubes containing 25 ml of filtered lake water (Whatman GF/C).

For analysis of phytoplankton photosynthetic rate, 25 ml water samples from each station were dispensed into 15 clear and 3 darkened test tubes. All epiphyton and phytoplankton test tubes were inoculated with $NaH^{14}CO_3$. Three clear test tubes were placed in each range of irradiance for a 2 h incubation. A LiCor spherical quantum sensor (Model LI-193SA) was used to determine irradiance. Three darkened test tubes were placed at the back of the incubator for 2 h to measure dark ^{14}C uptake. After incubation, samples were filtered onto Whatman GF/C filters and fumed over concentrated HCl for 5 min to liberate residual inorganic ^{14}C. Radioactivity of the filters and Nitex squares was determined with a liquid scintillation counter and the rate of specific (chl*a* normalized) photosynthesis (Ps) was calculated with the formula:

$$Ps\ (\mu g\ carbon\ (C)\cdot\mu g\ chl a^{-1}\cdot hr^{-1}) = dpm_S\cdot C\cdot 1.05\cdot(dpm_T\cdot T\cdot chl a)^{-1}$$

where dpm_S and dpm_T are the radioactivity of each sample corrected for dark uptake and of added ^{14}C, respectively; C is the measured DIC of the lake water; 1.05 is an isotopic discrimination factor (Strickland and Parsons 1972); T is incubation time (h); and chl*a* is a measure of algal biomass ($\mu g\cdot L^{-1}$ or $\mu g\cdot cm^{-2}$). The 15 specific rates of photosynthesis derived for each station were plotted against the irradiance to which the test tubes were exposed to determine chl*a* specific parameters $Pmax_b$ (maximum optimal rate of photosynthesis), $alpha_b$ (slope of the light dependent portion of the P/I curve) and $beta_b$ (slope of the light inhibited portion of the P/I curve) with a curve fitting function (Sigma Plot Version 2.0) and the equation of Platt et al. (1980). I_k, the half-saturation constant for light, was calculated as $Pmax_b$ divided by $alpha_b$. Mean daily rates of photosynthesis ($mgC\cdot m^{-3}\cdot d^{-1}$ for phytoplankton or $mgC\cdot m^{-2}$ substrata$\cdot d^{-1}$ for epiphyton) were determined throughout the sampling season (June 1st to September 15th) by numerical integration

(YPHOTO, version 4.0, Fee 1990) over depth and time of day from $Pmax_b$ and $alpha_b$, algal biomass (as chl*a*) and E_{PAR}. Ambient PAR was estimated assuming 70% cloudless conditions (YPHOTO, version 4.0, Fee 1990). Mean daily rates of epiphyton photosynthesis ($mgC \cdot m^{-2}$ substrata$\cdot d^{-1}$) were multiplied by the estimated amount of submersed macrophyte surface area available on each day during the sampling season (Appendix 1) to produce daily estimates of the rate of epiphyton photosynthesis per m^2 of lake surface area. Mean daily rates of epiphyton and littoral photosynthesis were multiplied by surface area or volume of the littoral zone, respectively, to produce daily estimates of photosynthesis (mgC), and summed over the sampling season to provide an estimate of total littoral algal photosynthesis (mgC). Daily rates of pelagic phytoplankton photosynthesis were multiplied by volume of the pelagic zone to produce daily estimates of photosynthesis (mgC), and summed over the sampling period to provide an estimate of total pelagic algal photosynthesis (mgC). The percent contribution of littoral algae to whole-lake algal photosynthesis was calculated for each study lake and compared with values derived from published data for seven lakes: Lake Kalgaard (Sondergaard and Sand-Jensen 1978), Paajarvi (Kairesalo 1980), Lake Wingra (Jones 1984), Lawrence Lake (Wetzel et al. 1972), Lake Ohrid (Allen and Ocevski 1981), Hastings Lake (Jenkerson and Hickman 1986), Lake Belau (Gessner et al. 1996).

3.1.5 Macroinvertebrates

In June, one piece of Nitex fabric from each station in every lake was preserved in 4% formalin solution and stored for analysis of macroinvertebrates. Macroinvertebrates were identified under a low power dissecting microscope to family, subclass or order

following keys by Clifford (1991). Potentially herbivorous macroinvertebrates were identified and all others were excluded from subsequent analysis.

3.1.6 TROLS sampling

Concurrent with this study, the larger TROLS project sampled the same study lakes at the point of maximum depth within 1 to 9 d of each visit for this study (Prepas et al. in prep). However, TROLS water samples were collected from the euphotic zone which was defined as the zone from the surface to the depth of 1% of surface irradiance measured with a LiCor quantum sensor (Model LI-192SA). Except in August, TROLS euphotic zone samples were within 0.5 m of depths sampled in this study. In August, in SPH 20 and 200, TROLS euphotic samples were 3 and 1 m deeper, respectively, than depths sampled in this study. SPH 100 and 800 were sampled 1 m deeper in this study than TROLS euphotic samples in August. With the exception of the method for measuring phytoplankton chl*a* (95% cold ethanol method of Bergmann and Peters 1980), the TROLS project used the same methodologies for water chemical analyses. Since particulate nitrogen (PN) was not measured in this study, TROLS PN data from June, July and August were added to TDN concentration from this study to determine total nitrogen (TN). The TROLS project also measured water temperature every 14 d at 1 m intervals through the water column of each study lake at the point of maximum depth with a YSI model 57 DO/temperature meter. The thermocline was defined as the depth at which the rate of decrease in temperature was greater than or equal to $1°C \cdot m^{-1}$. When a thermocline existed, the water column was described as stratified. In the absence of a thermocline, the water column was described as mixed. Mixing zone was defined as the surface to the depth of the thermocline or the bottom of the lake when the lake was

mixed. The ratio of euphotic to mixing zone depth was calculated for each lake in every month.

3.1.7 Statistical analyses

Nonnormal data were $\log_{10}(X+1)$ or arcsin X (percent data) transformed where necessary to meet the assumptions of normal distribution. Nonparametric statistics were employed when transformed data were not normally distributed. Comparisons between pelagic water chemistry and phytoplankton biomass estimates made by TROLS and this study ($n = 16$), and those made between littoral and pelagic water chemistry, E_{PAR}, and phytoplankton photosynthesis parameters and biomass ($n = 16$) were made with either a paired *t*-test (normally distributed data) or a Wilcoxon Signed-Rank test (nonparametric data). Water chemistry, E_{PAR} and littoral algal parameters during periods of mixing ($n = 30$) and stratification ($n = 66$) were compared with a *t*-test (normally distributed data) or a Mann-Whitney test (non-parametric). Relationships between water chemistry and algal photosynthesis and biomass parameters were examined with Spearman's rank correlation. Nested ANOVA was used to determine the influence of lake, sampling month, transect and station on epiphyton biomass. Although epiphyton biomass data were not normally distributed, sample size was high ($n = 576$) and thus data were suitable for ANOVA (Zar 1974). Relationships between study and literature lake morphometric variables and contribution of the littoral zone to algal photosynthesis were explored with linear regression analysis and Pearson product-moment correlation. Differences were considered significant if $P < 0.05$.

3.2 Results

Water column vertical temperature profiles indicate that while SPH 200 was thermally stratified during each sampling period, SPH 20, 100 and 800 underwent periodic mixing. SPH 20 mixed during the September sampling period, while SPH 800 was stratified only during the July sampling period. SPH 100 was stratified during June, early July, and August but mixed completely in September. SPH 100 also mixed completely in late July although the mixing event did not coincide with sampling for this study. Therefore, SPH 20 and 200 are described as stratified while SPH 100 and 800 are polymictic.

E_{PAR} was between 33 and 250% higher in the shallow lakes, SPH 100 and 800 as compared to the deep lakes, SPH 20 and 200. In addition, median littoral E_{PAR} was on average 50% higher than in the pelagic zone ($n = 16$, $P < 0.02$, Tables 3.2 and 3.3). Although differences were not statistically significant ($n = 16$, $P > 0.05$), median littoral and pelagic E_{PAR} were 31 and 57% higher, respectively, during periods of mixing as compared to stratification (Table 3.4).

Seasonal and between lake variation in light penetration and mixing regime resulted in a large range in the ratio of euphotic to mixing zone depth (0.4 to 2.2). All of the study lakes had periods where the ratio of euphotic to mixing zone depth (Z_E/Z_M) was above and below 1. However, Z_E/Z_M tended to be highest in June and decline over the summer to reach a minimum in September.

Except for pH and DOC, no detectable differences or patterns between pelagic water chemistry data from this study and the TROLS project were observed ($P > 0.05$). pH was higher in the TROLS samples with a mean of 8.1 compared to 7.6 in this study (P

< 0.02). Samples for this study were collected earlier in the day (on average between 730 and 1100 h) as compared to TROLS samples. DOC was also slightly higher in the TROLS samples with a mean of 12.9 compared to 12.3 $mg \cdot L^{-1}$ in this study ($P < 0.001$) and may reflect the different parts of the water columns sampled in the two studies. Therefore, pelagic water chemistry measurements from this study are effectively interchangeable to those from the TROLS project.

With the exception of TP, no detectable differences or patterns were observed between littoral (Table 3.2) and pelagic (Table 3.3) water chemistry variables. Median littoral TP concentration was on average 38% higher than in the pelagic zone ($P < 0.001$). Median summer littoral nutrient concentrations suggest that the study lakes are eutrophic with TP concentrations ranging between 34 and 140 $\mu g \cdot L^{-1}$ (Table 3.2). Littoral TP concentrations were two to four times higher in the two shallower lakes (SPH 100 and 800) as compared to the deeper lakes (SPH 20 and 200). High TP concentrations in the littoral zones of all four study lakes suggest the potential for high algal photosynthesis.

Comparison of littoral water chemistry variables in all study lakes during periods of mixing ($n = 30$) and thermal stratification ($n = 66$) suggests differences. Median TP, PP and DOC concentrations were between 10 and 115% higher when the lakes were thermally mixed ($n = 30$) rather than stratified ($n = 66$) during sampling ($P < 0.01$). In contrast, median DIC concentrations were 6% higher during periods of stratification as compared to mixing ($P < 0.02$). However, for the remaining water chemistry variables, no detectable differences were observed between periods of stratification and mixing. When periods of stratification and mixing were compared within lakes ($n = 24$), few detectable differences occurred. However, patterns of higher TP and PP concentrations

during periods of mixing were the same in SPH 20 and 800 as those observed across the entire data set. In contrast, in SPH 100, higher TP and PP concentrations were measured during stratification rather than mixing. Although both TP and PP were higher during periods of mixing as compared to stratification across the entire data set and in SPH 20 and 800, an opposite pattern in SPH 100 suggests that trends were not consistent.

Herbivorous macroinvertebrate counts in June were dominated by larval chironomids in all four lakes. SPH 20 and 800 had lower chironomid counts (mean 12 and 8.8 organisms per Nitex, respectively) than SPH 200 and 100 (mean 36 and 40 organisms per Nitex, respectively). Although SPH 800 had 8 different taxa of herbivorous macroinvertebrates, except for chironomids, organism counts were low. In contrast, samples from SPH 100 contained only chironomids and Ostracoda while SPH 20 samples had chironomids, Ostracoda and Plecoptera. In SPH 200, herbivorous macroinvertebrate samples consisted primarily of chironomids although 4 Planorbidae were also found. Mean number of herbivorous macroinvertebrates per Nitex was highest in SPH 100 (49 organisms per Nitex), moderate in SPH 200 (31 organisms per Nitex) and lowest in SPH 20 (13 organisms per Nitex) and 800 (8.5 organisms per Nitex).

Spatial and temporal distribution of epiphyton biomass in the study lakes indicated differences in time and space within lakes, but not between lakes (Table 3.5). However, both sample size (n = 4 lakes) and power ($\beta = 0.6$) were low for comparison between lakes. Most of the variability in epiphyton biomass occurred over time (39%) followed by differences between replicates (34%). Although epiphyton biomass ranged between 0.01 and 30.9 $\mu g \cdot cm^{-2}$, 75% of the values were less than 2.4 $\mu g \cdot cm^{-2}$. No detectable differences occurred in epiphyton biomass during periods of stratification (n =

66) and mixing ($n = 30$). Epiphyton biomass and TDP concentration were positively correlated ($r_s = 0.46$, $P < 0.0001$). In addition, a weak positive relationship existed between epiphyton biomass and TP concentration ($r_s = 0.23$, $P = 0.03$). Although representative samples from the lakes require time series estimates over the growing season, spatial variability in epiphyton biomass within each lake appears to be less significant.

Median phytoplankton biomass was higher on average in the littoral zone as compared to the pelagic ($n = 16$, $P < 0.001$). However when lakes were examined individually, littoral phytoplankton biomass greatly exceeded that of the pelagic in SPH 20, 200 and 800 while in SPH 100, higher median phytoplankton biomass was found in the pelagic zone. Median littoral phytoplankton biomass was 250% higher during periods of mixing ($n = 30$) as compared to stratification ($n = 66$) ($P < 0.01$). Despite different methodologies, estimates of phytoplankton biomass as chl*a* showed no detectable differences between the TROLS project and this study ($P > 0.2$).

Chlorophyll *a*-specific photosynthesis-irradiance curves yielded on average higher $Pmax_b$ and $alpha_b$ values for phytoplankton as compared to epiphyton (Table 3.7). Median phytoplankton $Pmax_b$ (4.1 $mgC \cdot mgChla^{-1} \cdot h^{-1}$) and $alpha_b$ (0.027 $mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$) are within the range of values reported in the literature (Harris 1978, Platt et al. 1980, Robinson et al. 1997, Carignan et al. 2000). Literature values for periphyton are less common but comparisons again suggest that median $Pmax_b$ (1.0 $mgC \cdot mgChla^{-1} \cdot h^{-1}$) and $alpha_b$ (0.004 $mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$) are within the range reported for algae attached to artificial substrata (Hill and Boston 1991, Robinson et al. 1997).

Volumetric rates of phytoplankton photosynthesis ($mgC \cdot m^{-3} \cdot d^{-1}$) were on average 50% higher in the littoral than in the pelagic zone (n =16, P<0.0001) (Table 3.6) with the greatest differences observed in the deepest lakes, SPH 20 and 200. Although no detectable differences were observed in the photosynthesis parameters ($Pmax_b$ or $alpha_b$ Table 3.7, $P > 0.05$), $Pmax_b$ was slightly higher in the littoral zone as compared to the pelagic in SPH 20 and 200. Higher rates of volumetric littoral phytoplankton photosynthesis as compared to the pelagic zone appear to correspond with both higher phytoplankton biomass and $Pmax_b$.

Comparisons of littoral phytoplankton and epiphyton photosynthesis parameters in all study lakes during periods of mixing (n = 30) and thermal stratification (n = 66) suggests differences. Although median volumetric phytoplankton photosynthetic rate ($mgC \cdot m^{-3} \cdot d^{-1}$) was 184% higher during periods of mixing as compared to stratification (P 0.03), no differences were detected in phytoplankton $Pmax_b$. In addition, median epiphyton and littoral phytoplankton $alpha_b$ values during mixing were more than 30% higher than those during stratification ($P < 0.004$ and 0.02, respectively). However, epiphyton photosynthetic rate, and $Pmax_b$ were not detectablely different during periods of stratification and mixing. When periods of stratification and mixing were compared within lakes (n = 24), few detectable differences occurred. However, patterns of higher phytoplankton and epiphyton $alpha_b$ during periods of mixing were the same in SPH 20 and 800 as those observed across the entire data set. In contrast, in SPH 100, higher phytoplankton $alpha_b$ were measured during stratification rather than mixing. Although algal parameters were generally higher during periods of mixing rather than stratification, trends observed across the data set were not consistent within lakes.

Mean daily rates of littoral volumetric phytoplankton photosynthesis were correlated with more water column variables than rates of epiphyton photosynthesis (n = 86, Table 3.8). Littoral phytoplankton, but not epiphyton, photosynthetic rate was related to E_{PAR}, and TN, TP, and PP concentration. Phytoplankton biomass was also positively correlated with E_{PAR} suggesting that a portion of light extinction in the water column was due to phytoplankton. Littoral phytoplankton photosynthesis was also positively correlated with epiphyton biomass (r_s = 0.22, P <0.05). However, littoral volumetric phytoplankton and epiphyton rates of photosynthesis were both positively related to biomass (Figures 3.2 and 3.3) and TDP concentration suggesting that the same variables limit attached and free-floating algal photosynthesis in the study lakes.

Nevertheless, there was no detectable relationship between epiphyton photosynthetic rate and TDP concentration in SPH 200 (n = 24, P > 0.5) or during periods of mixing (n = 30, P > 0.45). Epiphyton photosynthetic rate in SPH 200 was not correlated with any of the water chemistry variables, E_{PAR}, or either epiphyton or phytoplankton biomass. Therefore, a variable that was not accounted for in this study was influential in SPH 200. During periods of mixing, epiphyton photosynthetic rate was not related to TDP concentration and was negatively correlated with phytoplankton biomass, and TP and PP concentration (Table 3.9). In contrast, during periods of thermal stratification, epiphyton photosynthetic rate was positively related to TDP concentration and both TP and PP concentration. Although, in general, epiphyton photosynthetic rate was positively correlated with TDP concentration, the relationship was not consistent in SPH 200, or during mixing where trends were reversed as compared to stratification.

Areal pelagic phytoplankton photosynthetic rate ($mgC \cdot m^{-2} \cdot d^{-1}$) was negatively related to Z_E/Z_M suggesting that light penetration is controlled by algal biomass within the mixed layer ($r^2 = 0.37$, $P < 0.04$). Pelagic phytoplankton $alpha_b$ was also negatively correlated with Z_E/Z_M ($r^2 = 0.70$, $P < 0.001$) indicating that phytoplankton are adapted to shade at low Z_E/Z_M, although the negative relationship between Z_E/Z_M and pelagic phytoplankton $Pmax_b$ ($r^2 = 0.45$, $P < 0.02$) implies that temperature may also be a factor. Enhanced rates of photosynthesis at low as compared to high Z_E/Z_M, may have resulted in higher biomass ($mg \cdot m^{-2}$) since pelagic phytoplankton biomass is also negatively related to Z_E/Z_M ($r^2 = 0.35$, $P < 0.05$). Despite lower light in the mixed layer at low as compared to high Z_E/Z_M, higher pelagic phytoplankton $alpha_b$ and $Pmax_b$ lead to higher photosynthetic rates.

In the study lakes, contribution of the littoral zone to whole-lake algal photosynthesis (mgC) was inversely related to lake depth. In SPH 20, the deepest of the study lakes, pelagic contributions to algal photosynthesis dominated, and littoral phytoplankton photosynthesis was double that of epiphyton (Figure 3.4). Again, pelagic phytoplankton contributed the most to algal photosynthesis in SPH 200. In SPH 100 and 800, the shallowest of the study lakes, epiphyton photosynthesis was 3 and 4 times higher than pelagic phytoplankton, respectively. Except in SPH 20, the contribution of the littoral zone to whole-lake algal photosynthesis (mgC) exceeded that of the pelagic (Table 3.10).

Although in this study, percent contribution of littoral algae to whole-lake algal photosynthesis appeared to depend on lake depth, when the lakes from the literature were included (Table 3.10), no detectable relationship existed with either mean or maximum

depth ($P > 0.1$). However, a positive relationship existed between littoral surface area and contribution to whole-lake algal photosynthesis ($r^2 = 0.90$, $P < 0.0001$, Figure 3.5). Despite vast differences between lakes with respect to mean and maximum depth, geographical location, trophic classification, and macrophyte density, the contribution of littoral algae to whole-lake algal photosynthesis can be predicted from the surface area of the littoral zone.

3.3 Discussion

As could be expected, rates of phytoplankton photosynthesis were related to more water column variables than rates of epiphyton photosynthesis. Attached algae are characterized by a greater efficiency of nutrient recycling and retention than phytoplankton (Wetzel 1996) leading to less dependence on, and correlation with, external nutrient sources. However, some relationships between phytoplankton photosynthesis and total and particulate phosphorus and nitrogen concentration are spurious since suspended particles include phytoplankton cells. Furthermore, phytoplankton cells contributed to decreasing light penetration in the water column as is indicated by the positive correlation between light extinction and phytoplankton biomass. Therefore, the lack of a distinguishable relationship between epiphyton photosynthesis and TN, PN, TP and PP concentration may be due to intense recycling within boundary layers.

A positive correlation between the rate of epiphyton photosynthesis and TDP concentration is one not previously noted in the literature. Previous authors have focused on the correlation between epiphyton, particularly biomass, and TP, rather than TDP concentration. In one study, the relationship between epiphyton biomass and TP was

positive at low TP (< 39 $\mu g \cdot L^{-1}$) and negative at high TP (39 - 73 $\mu g \cdot L^{-1}$) concentration (Lalonde and Downing 1991). Spatially and temporally (range TP 15 to 312 $\mu g \cdot L^{-1}$), a weak positive relationship was observed between epiphyton biomass and TP, a stronger positive relationship existed between TDP and both epiphyton photosynthesis and biomass.

However, when periods of stratification were separated from periods of mixing, the positive relationship between TDP and both epiphyton photosynthesis and biomass existed only during periods of stratification. I hypothesize that during periods of mixing, increased suspended matter impedes light transmission to epiphyton leading to poor correlation with water column variables. During stratification, reduced suspended matter enhances light penetration and epiphyton photosynthesis. The relationship between epiphyton photosynthesis and TDP during periods of stratification suggests phosphorus limitation. Higher littoral TP and PP concentration, phytoplankton biomass, and both epiphyton and phytoplankton $alpha_b$ during periods of mixing as compared to stratification support the hypothesis. Muller (1995) also noted an influence of stratification vs. mixing when examining the relationship between epiphyton photosynthesis and biomass. She attributed the larger increase in photosynthesis with increases in chl*a* to higher water temperatures during stratification as shown by higher $Pmax_b$, $alpha_b$ and Ik values. In contrast in my study lakes, the absence of a detectable difference in $Pmax_b$, coupled with a higher $alpha_b$ during mixing, suggests that epiphyton are adapted to changes in irradiance rather than water temperature.

In general, comparison across the four study lakes provided the best representation of potential light limitation of epiphyton during mixing and phosphorus

limitation during stratification. When the lakes were examined individually, SPH 20 and 800 demonstrated the same patterns as the entire data set with higher TP and PP concentration, and phytoplankton biomass during mixing as compared to stratification. Since SPH 200 is stratified for the entire study, no periods of mixing exist for comparison. Although the patterns are reversed in SPH 100, periods of stratification in shallow SPH 100 are likely too short to influence TP and PP concentration, and phytoplankton biomass. Nutrient enrichment experiments could provide a clearer picture as to how epiphyton will respond to changes in TP and TDP.

In SPH 200, where stratification persisted for the entire sampling season, the rate of epiphyton photosynthesis was not correlated with any of the water column variables or with epiphyton or phytoplankton biomass. However, grazing pressure may have strongly influenced epiphyton photosynthetic rate and biomass in SPH 200. Previous studies have suggested that although moderate grazing pressure may reduce periphyton biomass, photosynthesis may be stimulated by the removal of dead or senescent algal cells allowing higher light penetration to lower strata of the epiphytic mat (Lamberti et al. 1987). Therefore, relationships between epiphyton photosynthetic rate and biomass would be weaker under conditions of moderate as compared to high or low grazing pressure.

The hypothesis of moderate grazing pressure on epiphyton in SPH 200 as compared to the other study lakes is supported through isotope and dietary analysis, numbers of macroinvertebrates, and phaeopigment to chl*a* ratios. Beaudoin's (1998) isotope and dietary analysis of food webs in SPH 200 indicated a strong dependence of the only fish species in the lake, northern pike (*Esox lucius*), on littoral invertebrate prey.

She suggests that northern pike in SPH 200 are at the top of a littoral food chain driven by non-phytoplankton primary producers, possibly epiphyton. In this study, support for moderate grazing of epiphyton in SPH 200 was provided by counts of the mean number of herbivorous macroinvertebrates in June. Finally, the amount of phaeopigment relative to chl*a* in SPH 200 is slightly lower than in the other study lakes ($P < 0.001$) suggesting a constant removal of dead and senescent cells allowing the remaining algal cells to maintain high rates of photosynthesis despite low biomass. Although physical sloughing of dead and senescent algal cells can occur through turbulence, placement of the artificial substrata below the maximum depth of surface waves should limit disturbance. However, grazing pressure has been shown to result in the removal of dead or senescent algal cells through sloughing (Lamberti et al. 1987). Although moderate grazing of epiphyton in SPH 200 may have resulted in the absence of a detectable relationship between epiphyton photosynthetic rate and both algal biomass and water column variables, further experiments to assess grazing pressure are recommended.

To estimate daily epiphyton photosynthetic rates in the study lakes, epiphyton parameters determined for samples incubated at 0.5 m depth were extrapolated to the rest of the water column. Although Allen and Ocevski (1981) noted uniform distribution of epiphyton biomass with increasing depth in oligotrophic Lake Ohrid, other authors have suggested that epiphyton biomass will be lower at the surface due to higher wave action and desiccation from fluctuations in water level (Muller 1995, Robinson et al. 1997). However, epiphyton biomass may decline with depth due to decreasing light penetration (Lalonde and Downing 1991) or be reduced at the sediment surface due to higher gastropod grazing pressure (Muller 1995). In eutrophic Lake Belau, a small lake with

similar fetch to the study lakes, Muller (1995) noted maximum epiphyton biomass between 0.1 and 0.5 m depth. Placement of substrata at 0.5 m in the study lakes may have also resulted in maximum biomass due to avoidance of wave and wind action, desiccation, severe light extinction and maximum gastropod grazing. Extrapolation of alpha and Pmax to all depths in this study is likely valid since Jones (1984) failed to demonstrate depth variations in the photosynthesis parameters in shallow, eutrophic Lake Wingra, a lake of similar surface area to the study lakes. Although rates of epiphyton photosynthesis have been observed to decline with depth (Cattaneo and Kalff 1980), this was attributed to decreasing irradiance. In this study, the influence of reduced light penetration with increasing depth was accounted for by the model that derived daily rates of epiphyton photosynthesis. Therefore, in the shallow and small, eutrophic lakes of the Boreal Plain, extrapolation of epiphyton biomass, alpha and Pmax with depth presumably lead to accurate estimates of epiphyton photosynthesis which compared favorably with those in the literature (Allen and Ocevski 1981, Jones 1984, Gessner et al. 1996, Raspopov et al. 1996).

Epiphyton photosynthesis and biomass in this study were estimated on artificial substrata resulting in several implications for whole-lake extrapolation. Previous research has debated the use of artificial substrate to emulate macrophyte hosts since it is hypothesized that the macrophyte and its epiphytes undergo a complex interaction (Wetzel 1983b, Harrison and Durance 1985, Burkholder and Wetzel 1990). However, Eminson and Moss (1980) suggest that the degree of positive macrophyte-epiphyte interaction depends on water nutrient status such that interactions are critical in oligotrophic lakes and minimal in eutrophic lakes. Since the study lakes are eutrophic,

macrophyte-epiphyte interactions are expected to be minimal. Although some previous authors have suggested that macrophyte architecture influences epiphyton development and biomass (Cattaneo and Kalff 1980, Allen and Ocevski 1981), Lalonde and Downing (1991) suggested that differences in the quantity of epiphyton biomass were related to macrophyte habitat characteristics. They concluded that environmental and seasonal factors had a greater influence on development of epiphyton biomass than macrophyte structure. In addition, the use of artificial substrata may have been advantageous since previous studies demonstrate decreased variability in chl*a* estimates on artificial as compared to natural substrata (Morin and Cattaneo 1992). Also, use of artificial substrata greatly improves sampling feasibility thereby allowing the first estimates of epiphyton photosynthetic rate and biomass in the remote study area. Therefore, sources of error associated with use of artificial substrata in the eutrophic study lakes were minimal and outweighed by advantages.

In the study lakes, volumetric rates of littoral phytoplankton photosynthesis exceeded those of the pelagic zone. Higher volumetric rates of littoral as compared to pelagic photosynthesis may be attributed to greater littoral phytoplankton biomass. Aggregation of phytoplankton within macrophyte beds could be due to wind and waves although such actions would be expected to primarily influence the downwind side of the lake. However, higher littoral as compared to pelagic phytoplankton biomass may be due to the contribution of detached algae from epiphytic or epipelic habitats. Lake nutrient concentrations may have also been a factor in the higher rate of littoral phytoplankton photosynthesis. Although phytoplankton can be suppressed in the littoral zone due to competition from macrophytes and periphyton (Phillips et al. 1978, Wetzel 1983a,

Hansson 1990), suppression is expected to decrease with increasing nutrient concentrations (Phillips et al. 1978). Therefore, in the eutrophic study lakes, phytoplankton may achieve optimal rates of photosynthesis despite competition from periphyton and macrophytes. However, the role of water temperature cannot be ruled out. Although littoral temperatures were not measured in this study, previous research suggests that they will exceed those of the pelagic. In Eau Galle, a eutrophic reservoir with a similar fetch to the study lakes, daytime littoral temperatures (between 1400 and 2000 hours) were about 2°C warmer than the upper 1 m of the pelagic zone, while nighttime littoral temperatures were similar to or 1°C cooler than those in the pelagic (James and Barko 1991). Therefore, mean temperature in the littoral zone of the study lakes could be detectablely warmer during the daytime and of similar temperature during the nighttime as compared to the upper 1 m of the pelagic zone. Although higher *in situ* rates of phytoplankton photosynthesis may be expected in the littoral zone as compared to the pelagic, laboratory incubations were completed at uniform temperatures and should have alleviated temperature effects. As such, models of whole-lake algal photosynthesis should consider lake trophic status, susceptibility to wind, presence of attached algae, and temperature gradients before extrapolating rates of pelagic algal photosynthesis to the littoral zone.

Future research should address several aspects of the model relating littoral surface area to its contribution to whole-lake algal photosynthesis. Only six of the eleven study lakes found in the literature had measurements of both littoral and pelagic phytoplankton photosynthesis which, as suggested by the results of this study, may differ considerably. Inclusion of more lakes with estimates of both littoral and pelagic

photosynthesis would allow refinement of the model. In addition, estimates of phytoplankton photosynthesis based on surface area may have contributed to the positive correlation between the two. Model testing should consider inclusion of further volumetric estimates of littoral and pelagic phytoplankton photosynthesis. When the littoral zone was not defined for the lakes from literature, estimates were based on the area of expected macrophyte colonization. Areal photographs and bathymetry would produce more accurate estimates of littoral surface area. Although the model ignored epipelic contributions to algal photosynthesis, they are expected to be minimal in lakes with dense macrophyte beds (Kairesalo 1980, Jenkerson and Hickman 1986). However, including epipelon would increase model accuracy. Through further development of the model, the strong positive relationship between littoral contribution to whole-lake algal photosynthesis and surface area can be enhanced.

Finally, based on the relationship between surface area and contribution to whole-lake algal photosynthesis, in what lakes might we expect littoral to exceed pelagic algal photosynthesis? The lack of a detectable relationship between either mean or maximum depth and contribution of the littoral zone to whole-lake algal photosynthesis across both the literature and study lakes suggests that shallow lakes are not necessarily dominated by the littoral. Four of the 11 lakes included in this analysis (Hastings, Lawrence, SPH 100 and SPH 800) have higher percent littoral as compared to pelagic algal photosynthesis. Although all four lakes are relatively shallow (mean depth < 6 m), other shallow lakes (SPH 200, Lake Wingra) have higher pelagic vs. littoral algal photosynthesis. Littoral contribution to whole-lake surface area is dependent on variables that influence macrophyte distribution such as underwater light quality and quantity (Chambers and

Prepas 1988), littoral slope (Duarte and Kalff 1990), nutrient status (Phillips et al. 1978), sediment characteristics (Duarte and Kalff 1990, Chambers and Prepas 1990), littoral grazers or their predators (Carpenter and Lodge 1986), and anthropogenic disturbances such as mechanical removal. Therefore, contribution of the littoral zone to whole-lake algal photosynthesis depends on variables that influence macrophyte distribution and density. High macrophyte density in SPH 100 and 800 likely contributes to the dominance of littoral algal photosynthesis whereas in shallow Lake Wingra, with low macrophyte density (Jones 1984), the reverse is true. The four lakes included in this analysis where littoral exceeds pelagic algal photosynthesis range in trophic classification from oligotrophic to eutrophic suggesting that nutrient status is not the determining factor. In conclusion, although shallow lakes are likely to have higher littoral relative to pelagic algal photosynthesis, favorable conditions for extensive and dense macrophyte beds are also essential for littoral dominance.

3.4 References

Allen, H.L. & Ocevski, B.T. 1981. Comparative primary productivity of algal epiphytes on three species of macrophyte in the littoral zone of Lake Ohrid, Yugoslavia. *Holarctic Ecology* 4:155-160.

Beaudoin, C.P. 1998. Stable isotope study of food webs in lakes of Alberta's boreal forest. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Bergmann, M. & Peters, R.H. 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus-chlorophyll-seston relationships. *Can. J. Fish. Aquat. Sci.* 37: 111-114.

Burkholder, J-A.M. & Wetzel, R.G. 1990. Epiphytic alkaline phosphatase on natural and artificial plants in an oligotrophic lake: Re-evaluation of the role of macrophytes as a phosphorus source for epiphytes. *Limnol. Oceanogr.* 35: 736-747.

Cattaneo, A. & Kalff, J. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnol. Oceanogr.* 25:280-9.

Carignan, R., Planas, D. & Vis, C. 2000. Planktonic production and respiration in oligotrophic Shield lakes. *Limnol. Oceanogr.* 45: 189-199.

Carpenter, S.R. & Lodge, D.M. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* 26: 341-370.

Chambers, P.A. & Prepas, E.E. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. *Can. J. Fish. Aquat. Sci.* 45: 1010-1017.

Chambers, P.A. & Prepas, E.E. 1990. Competition and coexistence in submerged aquatic plant communities: the effects of species interactions versus abiotic factors. *Freshwater Biol.* 23: 541-550.

Clifford, H.F. 1991. Aquatic Invertebrates of Alberta. The University of Alberta Press, Edmonton, Alberta, Canada. pp. 538.

Duarte, C. M. & Kalff, J. 1990. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. *Limnol. Oceanogr.* 31:1072-1080.

Emínson, D. & Moss, B. 1980. The composition and ecology of periphyton communities in freshwater. I. The influence of host type and external environment on community composition. *Br. Phycol. J.* 15: 429-446.

Fee, E.J. 1990. Computer program for calculating *in situ* phytoplankton photosynthesis. *Can. Tech. Rep. Fish. Aquat. Sci.* 1740:1-27.

Gessner, M.O., Schieferstein, B., Muller, U., Barkmann, S. & Lenfers, U.A. 1996. A partial budget of primary organic carbon flows in the littoral zone of a hardwater lake. *Aquat. Bot.* 55:93-105.

Greenberg, A.E., Clesceri, L.S. & Eaton, A.D. 1992. Standard Methods for the Examination of Water and Wastewater. 18th edition. American Public Health Association, American Water Works Association and Water Environment Federation.

Hansson, L-A. 1990. Quantifying the impact of periphytic algae on nutrient availability for phytoplankton. *Freshwater Biol.* 24: 265-273.

Harris, G. P. 1978. Photosynthesis, productivity and growth: The physiological ecology of phytoplankton. *Arch. Hydrobiol. Beih.* 10: 1-171.

Harrison, P.G. & Durance, C.D. 1985. Reductions in photosynthetic carbon uptake in epiphytic diatoms by water-soluble extracts of leaves of *Zostera marina*. *Marine Biology* 90: 117-119.

Hill, W.R. & Boston, H.L. 1991. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnol. Oceanogr.* 36: 1375-1389.

James, W.F. & Barko, J.W. 1991. Estimation of phosphorus exchange between littoral and pelagic zones during nighttime convective circulation. *Limnol. Oceanogr.* 36: 179-187.

Jenkerson, C.G. & Hickman, M. 1983. The spatial and temporal distribution of an epiphytic algal community in a shallow prairie-parkland lake - Alberta, Canada. *Holarctic Ecology* 6: 41-58.

Jenkerson, C.G. & Hickman, M. 1986. Interrelationships among the epipelon, epiphyton and phytoplankton in a eutrophic lake. *Int. Revue Ges. Hydrobiol.* 71(4):557-79.

Jones, R.C. 1984. Application of a primary production model to epiphytic algae in a shallow, eutrophic lake. *Ecology* 65: 1895-1903.

Kairesalo, T. 1980. Comparison of in situ photosynthetic activity of epiphytic, epipelic and planktonic algal communities in an oligotrophic lake, southern Finland. *J. Phycol.* 16:57-62.

Lalonde, S. & Downing, J.A. 1991. Epiphyton biomass is related to lake trophic status, depth and macrophyte architecture. *Can. J. Fish. Aquat. Sci.* 48:2285-91.

Lamberti, G.A., Ashkenas, L.R., Gregory, S.V. & Steinman, A.D. 1987. Effects of three herbivores on periphyton communities in laboratory streams. *J. N. Am. Benth. Soc.* 6:92-104.

Menzel, D.W. & Corwin, N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.* 10:280-282.

Mc mans, J.T. 1988. Seasonal changes in biomass and production of periphyton growing upon reed in Lake Maarsseveen I. *Arch. Hydrobiol.* 112:21-42.

Morin, A. & Cattaneo, A. 1992. Factors affecting sampling variability of freshwater periphyton and the power of periphyton studies. *Can. J. Fish. Aquat. Sci.* 49: 1695-1703.

Muller, U. 1995. Vertical zonation and production rates of epiphytic algae on *Phragmites australis*. *Freshwater Biol.* 34:69-80.

Platt, T., Gallegos, C.L. & Harrison, W.G. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* 38:687-701.

Phillips, G.L., Eminson, D. & Moss, B. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4:203-126.

Prepas, E.E. & Rigler, F.H. 1982. Improvements in quantifying the phosphorus concentration in lake water. *Can. J. Fish. Aquat. Sci.* 39:822-829.

Prepas, E.E., Pinel-Alloul, B., Planas, D., Methot, G., Paquet, S. & Reedyk, S. 2000. Forest harvest impacts on water quality and aquatic biota on the Boreal Plain: Introduction to the TROLS lake program. In prep.

Raspopov, I.M., Andronikova, I.N., Dotsenko, O.N., Kurashov, E.A., Letanskaya, G.I., Panov, V.E., Rychkova, M.A., Telesh, I.V., Tchernykh, O.A. & Vorontsov, F.F. 1996. Littoral zone of Lake Ladoga: ecological state evaluation. *Hydrobiologia* 322: 39-47.

Riber, H.H., Sorensen, J.P. & Schierup, H.-H. 1984. Primary productivity and biomass epiphytes on *Phragmites australis* in a eutrophic Danish lake. *Holarctic Ecology* 7:202-10.

Riber, H.H. & Wetzel, R.G. 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnol. Oceanogr.* 32:1181-94.

Robinson, G.G.C., Gurney, S.E. & Goldsborough, L.G. 1997. The primary productivity of benthic and planktonic algae in a prairie wetland under controlled water-level regimes. *Wetlands* 17:182-94.

Sartory, D.P. & Grobbelaar, J.U. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia* 114:177-87.

Schindler, D.W. 1978. Factors regulating production and standing crop in the world's freshwaters. *Limnol. Oceanogr.* 23: 478-486.

Smith, V.H. 1979. Nutrient dependence of primary productivity in lakes. *Limnol. Oceanogr.* 24:1051-64.

Stainton, M.P., Capel, M.J. & Armstrong, F.A.J. 1977. The chemical analysis of freshwater. 2nd edition. *Fish. Environ. Can. Misc. Spec. Publ.* 25:180pp.

Strickland, J.D.H. & Parsons, T.R. 1972. A Practical Handbook of Seawater Analysis. 2nd edition. Fisheries Research Board of Canada Bulletin 167, Ottawa, Canada.

Sondergaard, M. & Sand-Jensen, K. 1978. Total autotrophic production in oligotrophic, Lake Kalgaard, Denmark. *Verh. Internat. Verein. Limnol.* 20: 667-673.

Solorzano, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. *Limnol. Oceanogr.* 14: 799-801.

Wetzel, R.G. 1983a. Limnology, 2nd edition. Saunders College Publishing, Toronto, pp. 767.

Wetzel, R.G. 1983b. Attached algal-substrata interactions: fact or myth, and when and how? In Periphyton of Freshwater Ecosystems. Edited by R.G. Wetzel. DrW, Junk Publishers, Boston. pp.207-215.

Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. *Verh. Internat. Verein. Limnol.* 24:6-24.

Wetzel, R.G. 1993. Microcommunities and microgradients: Linking nutrient regeneration, microbial mutalism, and high sustained aquatic primary production. *Neth. J. Aquat. Ecol.* 27:3-9.

Wetzel, R.G., Rich, P.H., Miller, M.C. & Allen, H.L. 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. *Mem. Ist. Ital. Idrobiol.* 29(Suppl.)185-243.

Zar, J.H., 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Table 3.1: Drainage basin and lake characteristics (E.E. Prepas, unpublished), and mean August macrophyte density.

Lake	Drainage Basin area (ha)	Lake Volume ($10^3 m^3$)	Mean depth (m)	Ratio of littoral to pelagic volume	% Watershed harvested	Macrophyte density (g of dry weight $\cdot m^{-2}$)
SPH 20	1002	7389	4.6	0.10	30	43
SPH 100	702	809	1.4	1.23	15	734
SPH 200	953	1304	3.3	0.28	18	163
SPH 800	619	1398	2.2	2.23	5	806

Table 3.2: Median and range (in parenthesis) of summer littoral nutrient concentrations, phytoplankton and epiphyton chl*a* concentration and light extinction in the study lakes (*n* = 24 per lake).

	SPH 20	SPH 100	SPH 200	SPH 800
TN/TP ratio	23 (59)	19 (21)	26 (62)	12 (32)
TDN/TDP ratio	61 (107)	31 (60)	70 (95)	55 (60)
NH_4^+ ($\mu g \cdot L^{-1}$)	13 (32)	186 (473)	158 (329)	13 (66)
$NO_3^- + NO_2^-$ ($\mu g \cdot L^{-1}$)	4 (5)	8 (22)	76 (220)	4 (10)
TDN ($\mu g \cdot L^{-1}$)	725 (528)	1147 (1083)	1002 (1127)	809 (669)
pH	7.4 (1.8)	7.5 (1.4)	7.6 (1.0)	8.3 (3.2)
DOC ($mg \cdot L^{-1}$)	10 (2)	13 (5)	13 (4)	14 (6)
DIC ($mg \cdot L^{-1}$)	24 (8)	23 (8)	41 (10)	23 (15)
TP ($\mu g \cdot L^{-1}$)	34 (91)	140 (243)	39 (87)	105 (162)
TDP ($\mu g \cdot L^{-1}$)	11 (10)	27 (34)	13 (12)	14 (19)
Si ($\mu g \cdot L^{-1}$)	1995 (944)	4808 (7133)	6103 (2349)	4073 (6397)
Phytoplankton Chl a ($\mu g \cdot L^{-1}$)	6 (40)	51 (168)	11 (30)	35 (233)
Epiphyton Chl a ($\mu g \cdot cm^{-2}$)	1.1 (2.2)	2.8 (26)	0.8 (3.3)	1.3 (3.7)
Epiphyton Phaeo ($\mu g \cdot cm^{-2}$)	3.5 (21)	11 (97)	2.3 (7.0)	3.4 (18)
E_{PAR}	1.9 (4.1)	2.9 (4.8)	1.7 (2.5)	3.1 (5.5)

Table 3.3: Median and range (in parenthesis) of summer pelagic nutrient concentrations, phytoplankton chl*a* concentration and light extinction in the study lakes (Except E_{PAR} (*n* = 4), n = 24 per lake).

	SPH 20	SPH 100	SPH 200	SPH 800
TDN/TDP ratio	60 (94)	24 (46)	69 (103)	40 (66)
NH_4^+ ($\mu g \cdot L^{-1}$)	9.4 (34)	234 (229)	177 (268)	12 (22)
$NO_3^- + NO_2^-$ ($\mu g \cdot L^{-1}$)	2.8 (2)	6.7 (7)	129 (192)	4.7 (11)
TDN ($\mu g \cdot L^{-1}$)	726 (545)	1174 (867)	961 (961)	829 (535)
pH	7.6 (1.7)	7.6 (3.6)	7.7 (0.6)	8.0 (2.4)
DOC ($mg \cdot L^{-1}$)	10 (2)	14 (5.7)	13 (4.9)	13 (3.4)
DIC ($mg \cdot L^{-1}$)	25 (6.4)	25 (13)	41 (12)	22 (15)
TP ($\mu g \cdot L^{-1}$)	23 (30)	128 (141)	33 (36)	60 (130)
TDP ($\mu g \cdot L^{-1}$)	8.9 (6.5)	25 (36)	13 (13)	13 (15)
Si ($\mu g \cdot L^{-1}$)	2147 (1193)	4690 (5684)	6156 (2128)	4675 (1333)
Phytoplankton Chl a ($\mu g \cdot L^{-1}$)	4.5 (8.0)	55 (88)	7.3 (12)	23 (66)
E_{PAR}	0.8 (1.0)	2.0 (5.1)	1.5 (0.3)	3.1 (2.1)

Table 3.4: Median and range (in parenthesis) of nutrient concentrations, algal parameters and light extinction in the study lakes during periods of mixing (n = 30) and stratification (n = 96).

	Mixed	Stratified
NH_4^+ ($\mu g \cdot L^{-1}$)	22 (482)	24 (332)
$NO_3^- + NO_2^-$ ($\mu g \cdot L^{-1}$)	4.6 (25)	5.1 (222)
TDN ($\mu g \cdot L^{-1}$)	851 (1188)	833 (1176)
pH	7.3 (3)	7.5 (2)
DOC ($mg \cdot L^{-1}$)	14 (6.8)	12 (6.4)
DIC ($mg \cdot L^{-1}$)	24 (15)	26 (29)
TP ($\mu g \cdot L^{-1}$)	119 (170)	55 (297)
TDP ($\mu g \cdot L^{-1}$)	17 (24)	13 (45)
Si ($\mu g \cdot L^{-1}$)	4184 (6477)	4494 (6359)
Phytoplankton Chl *a* ($\mu g \cdot L^{-1}$)	39 (233)	11 (169)
Phytoplankton $Pmax_b$ ($mgC \cdot mgChla^{-1} \cdot h^{-1}$)	4.1 (11.4)	4.1 (17)
Phytoplankton $alpha_b$ ($mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$)	0.03 (0.06)	0.02 (0.09)
Volumetric Phytoplankton Photosynthesis ($mgC \cdot m^{-3} \cdot d^{-1}$)	1808 (6936)	635 (1126)
Epiphyton Chl *a* ($\mu g \cdot L^{-1}$)	1.3 (3.7)	1.2 (27)
Epiphyton $Pmax_b$ ($mgC \cdot mgChla^{-1} \cdot h^{-1}$)	1.0 (1.4)	0.9 (4.4)
Epiphyton $alpha_b$ ($mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$)	0.005 (0.03)	0.004 (0.02)
Epiphyton Photosynthesis ($mgC \cdot m^{-2} \cdot d^{-1}$)	155 (809)	162 (762)
E_{PAR}	2.4 (5.5)	2.0 (5.3)

Table 3.5: Results of a nested ANOVA examining spatial and temporal variations in epiphyton biomass in the study lakes (% = percent variance component estimate).

Epiphyton Chla ($\mu g \cdot cm^{-2}$) n = 576	*P*	%
Lake	0.1766	12
Month[Lake]	<0.0001	39
Transect[Lake]	<0.0001	9
Station[Lake]	<0.0001	6
Error		34

Table 3.6: Mean summer pelagic and littoral phytoplankton photosynthesis (areal $mgC \cdot m^{-2} \cdot d^{-1}$ and volumetric $mgC \cdot m^{-3} \cdot d^{-1}$).

	Areal		Volumetric	
	Littoral	Pelagic	Littoral	Pelagic
SPH 20	436	718	397	239
SPH 100	4012	5542	3912	2771
SPH 200	549	919	546	306
SPH 800	2560	3304	2341	1652

Table 3.7: Median chl*a* normalized maximum optimal rate of photosynthesis ($Pmax_b$ $mgC \cdot mgChla^{-1} \cdot h^{-1}$) and efficiency of photosynthesis ($alpha_b$ $mgC \cdot mgChla^{-1} \cdot h^{-1} \cdot \mu mole^{-1} \cdot m^2 \cdot s^1$) for littoral and pelagic phytoplankton, and epiphyton (with range in parenthesis).

	Littoral phytoplankton		Pelagic phytoplankton		Epiphyton	
	$alpha_b$	$Pmax_b$	$alpha_b$	$Pmax_b$	$alpha_b$	$Pmax_b$
SPH 20	0.02	3.9	0.02	3.4	0.004	1.0
	(0.04)	(7)	(0.03)	(2.5)	(0.02)	(4.4)
SPH 100	0.03	4.8	0.03	5.7	0.004	0.9
	(0.08)	(15)	(0.04)	(4.6)	(0.02)	(2.5)
SPH 200	0.03	3.7	0.02	2.8	0.005	1.2
	(0.05)	(12)	(0.04)	(4.3)	(0.01)	(3.7)
SPH 800	0.02	4.2	0.04	6.1	0.004	1.0
	(0.07)	(12)	(0.05)	(6.3)	(0.03)	(1.3)

Table 3.8: Spearman rank correlation coefficients between epiphyton or phytoplankton mean daily photosynthesis and light extinction, water chemistry variables, and epiphyton and phytoplankton biomass (n = 86 except for PN and TN where n = 67).

	Epiphyton	Phytoplankton
E_{PAR}	-	0.61***
Log PN	-	0.79***
Log TN	-	0.43***
Log TP	-	0.86***
Log TDP	0.43***	0.55***
Log PP	-	0.85***
Log Phytoplankton Chla	-	0.82***
Log Epiphyton Chla	0.67***	0.22*

Note: "-" indicates not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$s

Table 3.9: Spearman rank correlation coefficients between epiphyton mean daily photosynthesis and light extinction, water chemistry variables, and epiphyton and phytoplankton biomass ($n = 61$ in stratified, $n = 28$ in mixed).

	Mixed	Stratified
E_{PAR}	-	-
Log TP	-0.39*	0.34**
Log TDP	-	0.51***
Log PP	-0.42*	0.33**
Log Phytoplankton Chla	-0.43*	-
Log Epiphyton Chla	0.73***	0.66***

Note: "-" indicates not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Table 3.10: Data obtained and derived from the study and literature lakes (values derived for this study are in bold).

Lake	Trophic class-ification	Extent of littoral zone	Mean depth (m)	Max depth (m)	% littoral surface area	Phytoplankton photosynthesis estimates based on...	% littoral photosynthesis	Littoral phytoplankton photosynthesis provided	Phytoplankton photosynthesis units
Lawrence Lake	oligo	0 - 5 m	5.9	12.6	**51**	surface area	**67**	No	$mg \cdot m^{-2} \cdot day^{-1}$
Lake Ohrid	oligo	**0 - 5 m**	145	298	**12**	surface area	**20**	Yes	$mg \cdot m^{-2} \cdot day^{-1}$
Lake Kalgaard	oligo	0 - 2 m	4.7	11	**23**	surface area	**24**	No	$mg \cdot m^{-2} \cdot day^{-1}$
Lake Paajavri	oligo	0 - 4 m	14	87	15	surface area	**20**	No	%
Lake Wingra	eutrophic	0 - 1.25 m	2.4	3.8	**29**	volume	**13**	No	$mg \cdot m^{-3} \cdot day^{-1}$
Hastings Lake	eutrophic	0 - 3 m	2.5	8	**66**	volume	**53**	No	%
Lake Belau	eutrophic	0 - 1.2 m	9	26	4.5	surface area	**2**	yes	$mg \cdot m^{-2} \cdot day^{-1}$
SPH 100	eutrophic	0 - 2 m	1.4	2.4	**71**	volume	**82**	yes	$mg \cdot m^{-3} \cdot day^{-1}$
SPH 20	eutrophic	0 - 3 m	4.6	8.4	**24**	volume	**22**	yes	$mg \cdot m^{-3} \cdot day^{-1}$
SPH 200	eutrophic	0 - 3 m	3.3	7.1	**43**	volume	**51**	yes	$mg \cdot m^{-3} \cdot day^{-1}$
SPH 800	eutrophic	0 - 3 m	2.2	3.4	**78**	volume	**93**	yes	$mg \cdot m^{-3} \cdot day^{-1}$

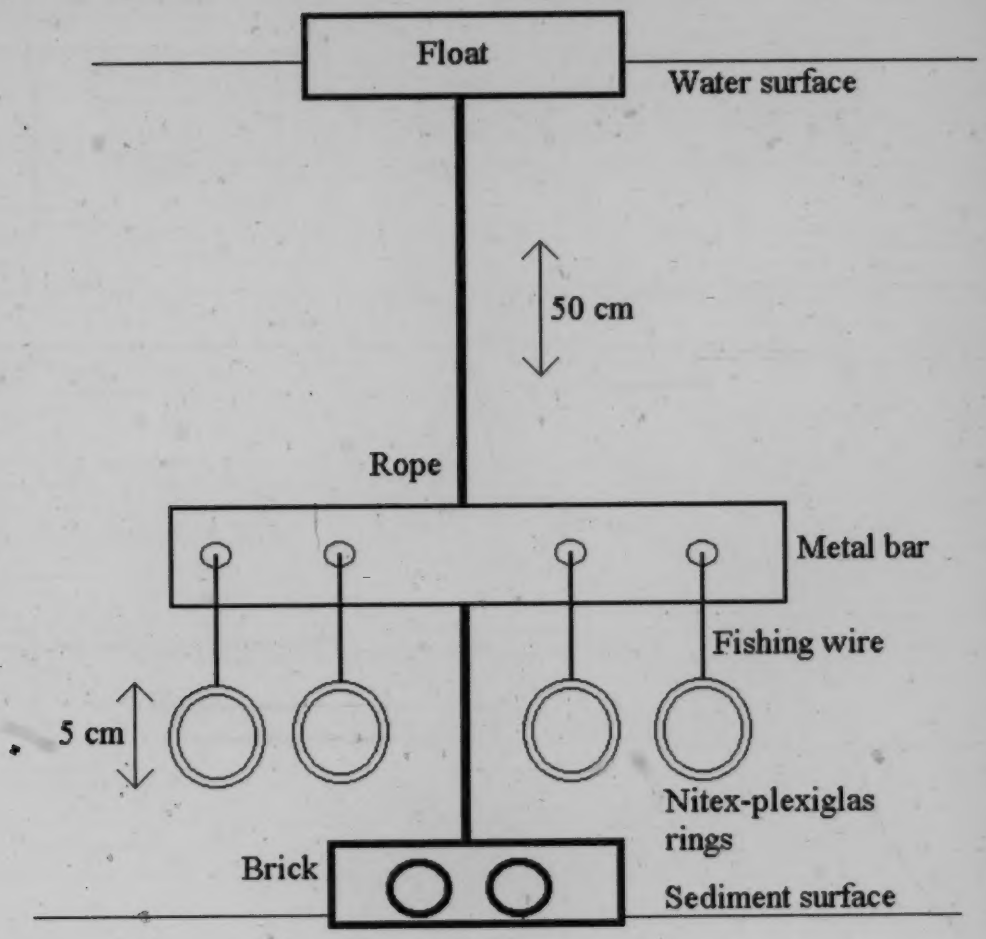


Figure 3.1: Schematic of the Nitex-Plexiglas rings.

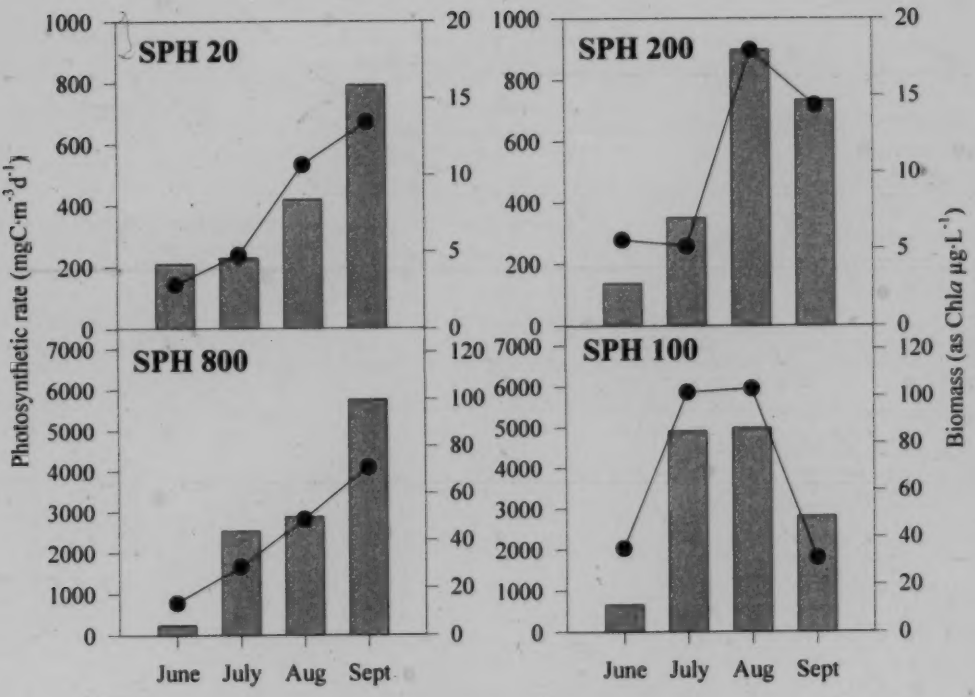


Figure 3.2: Seasonal changes in phytoplankton photosynthesis and biomass in the study lakes (Note: Scales are not the same).

Littoral phytoplankton biomass

Littoral phytoplankton photosynthesis

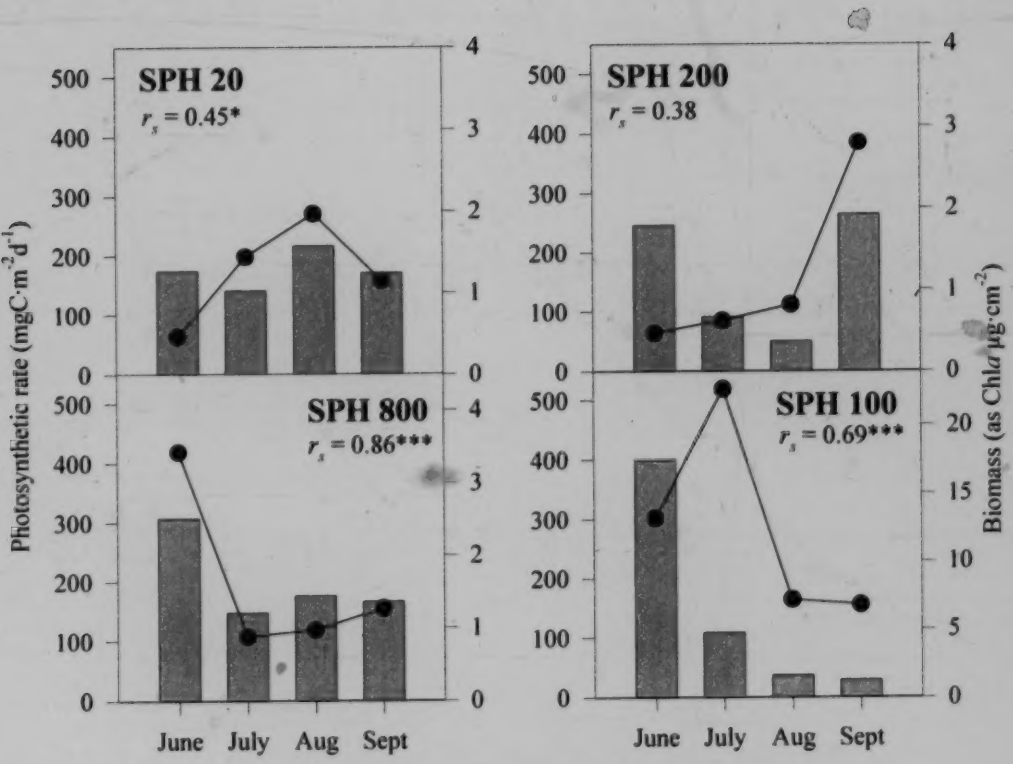


Figure 3.3: Seasonal changes in epiphyton photosynthesis and biomass in the study lakes with Spearman's rank correlation (r_s)
(* = probability < 0.05, ** = probability < 0.01,
*** = probability < 0.001; Note: Scales are not the same).
Epiphyton biomass
Epiphyton photosynthesis

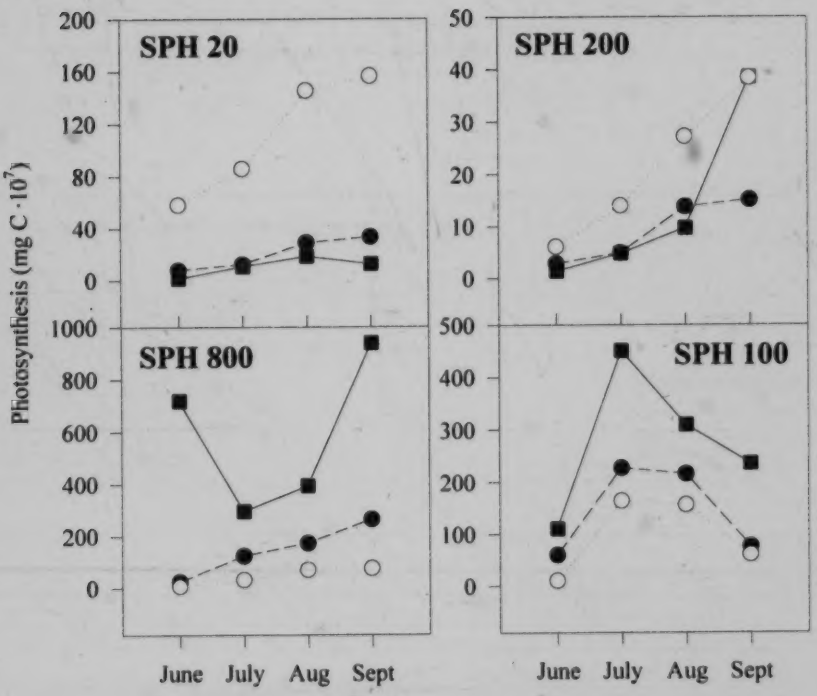


Figure 3.4: Contribution of epiphyton and both littoral and pelagic phytoplankton to whole-lake algal photosynthesis in the study lakes.

Epiphyton
Littoral phytoplankton
Pelagic phytoplankton

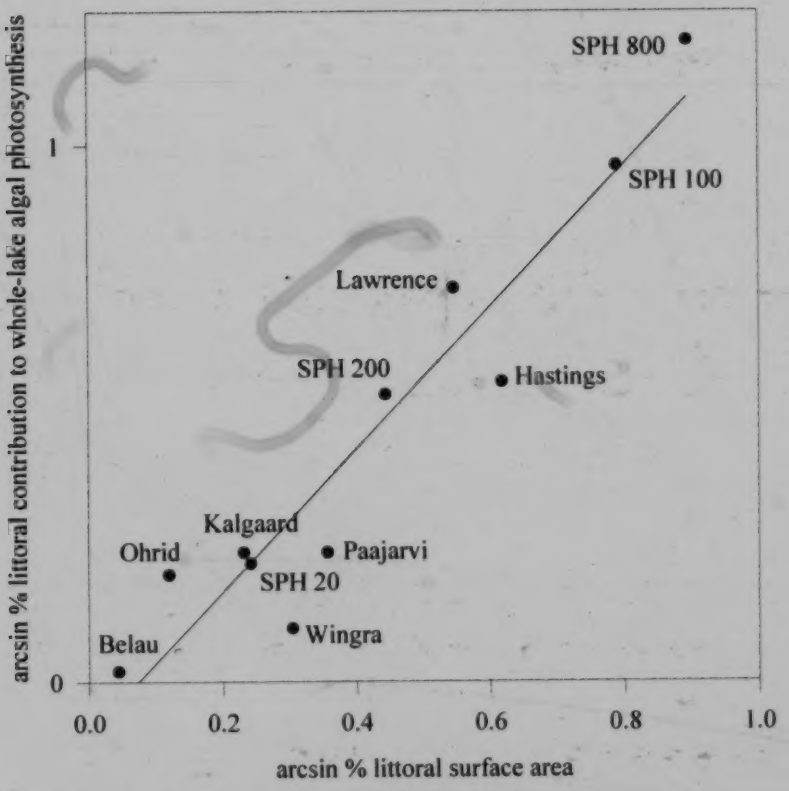


Figure 3.5: Plot of percent littoral contribution to whole-lake algal photosynthesis and surface area for 11 lakes with least squares regression line ($r^2 = 0.90$, $P < 0.0001$).

Chapter Four: Synthesis

4.0 Synthesis

The aim of this research was to determine the relative contributions of, and the variables influencing, littoral and pelagic algal photosynthesis in Boreal Plain lakes. Littoral algae play a critical role in lakes through provision of crucial carbon sources to higher trophic levels (Beaudoin 1998), regulation of nutrient fluxes (Wetzel 1990), competition (Phillips et al. 1978) and response to disturbance (Raspopov et al. 1996). Previous research suggests that the contribution of littoral algae to whole-lake algal photosynthesis depends on lake morphometry, and both macrophyte density and distribution (Kairesalo 1980, Jenkerson and Hickman 1986). Yet of the few studies providing measurements of both littoral and pelagic algal photosynthesis required to test this hypothesis, most focus on lakes dominated by the latter (Sondergaard and Sand-Jensen 1978, Kairesalo 1980, Allen and Ocevski 1981, Jones 1984, Gessner et al. 1996). In addition, projects examining the impact of disturbance on aquatic ecosystems are often focused on the pelagic zone. Knowledge of the contribution of littoral and pelagic algal photosynthesis will allow assessment of where study of the littoral zone is appropriate.

Although in this study, percent contribution of littoral algae to whole-lake algal photosynthesis appeared to depend on lake depth, when the lakes from the literature were included, no detectable relationship was found with either mean (range 1.4 to 145 m) or maximum (range 2.4 to 298 m) depth ($P > 0.1$). However, there was a positive relationship between littoral surface area and contribution to whole-lake algal photosynthesis ($r^2 = 0.90$, $P < 0.0001$). Despite vast differences between lakes with respect to distribution in the northern hemisphere, mean depth (range 1.4 to 145 m), trophic classification, and macrophyte density (SPH lakes 43 to 806 g dry weight·m^{-2}),

contribution of littoral algae to whole-lake algal photosynthesis was predicted from littoral surface area. While correlation between littoral surface area and contribution to algal photosynthesis indicates where littoral studies may be appropriate, refined estimates of littoral surface area and algal photosynthesis would enhance the relationship.

Phytoplankton photosynthetic rates in the littoral zone were consistently correlated with total dissolved phosphorus (TDP) concentration ($r_s = 0.55$, $P < 0.001$) while rates of epiphyton photosynthesis were only related to TDP concentration during periods of water column stratification ($r_s = 0.51$, $P < 0.001$). In contrast, during periods of water column mixing, a relationship was not detected between epiphyton photosynthetic rate and TDP concentration ($P > 0.45$). However, epiphyton photosynthesis was negatively correlated with phytoplankton biomass and both particulate and total phosphorus ($P < 0.05$). Periods of mixing had higher phytoplankton biomass, total and particulate phosphorus concentrations, and phytoplankton and epiphyton $alpha_b$ ($P < 0.01$) suggesting reduced light penetration to epiphyton. These results are consistent with phosphorus limitation of epiphyton during water column stratification and light limitation during mixing. However, nutrient-enrichment experiments would provide another opportunity to assess phosphorus vs. light limitation of littoral algae. Differences in the variables that influence epiphyton and phytoplankton photosynthesis suggest that their relative contribution to whole-lake algal photosynthesis might be influenced by changes in phosphorus concentration or light penetration.

Undetectable relationships between epiphyton photosynthesis and the measured biogeochemical variables in SPH 200 suggests that a variable not accounted for in this study was influential. Isotope and dietary analysis (Beaudoin 1998), moderate numbers

of macroinvertebrates (31 organisms per Nitex substrata as compared to 8.5, 13 and 41 organisms), and lower phaeopigment to chl*a* ratios ($P < 0.001$) suggest that moderate grazing pressure may have increased rates of photosynthesis (Lamberti et al. 1987) relative to the other study lakes. Therefore, the impact of grazer density on phosphorus and light limitation is a factor to consider in future efforts where appropriate.

In the study lakes, submersed macrophyte surface area for epiphyton colonization can be predicted from macrophyte biomass (r^2 range 0.34 to 0.96, $P< 0.03$). Macrophyte surface area to biomass relationships appear to be species-specific. General relationships for dissected and entire leaf macrophytes were not found. However, grouping of two morphologically similar species, *C. demersum* and *M. spicatum*, could be considered when converting macrophyte biomass to surface area. While lake-specific differences in the relationship between macrophyte surface area and biomass were only found for *C. demersum* in SPH 200, small sample sizes ($n = 15$) may have limited detection of differences. Dramatically fluctuating water levels and high ammonium concentration may have altered the relationship between *C. demersum* surface area and biomass in SPH 200 as compared to the other study lakes. Although relationships between macrophyte biomass and surface area can be used in estimating the contribution of epiphyton to whole-lake algal photosynthesis, deviations in lake-specific surface area to biomass correlation require subsequent attention.

4.1 References

Allen, H.L. & Ocevski, B.T. 1981. Comparative primary productivity of algal epiphytes on three species of macrophyte in the littoral zone of Lake Ohrid, Yugoslavia. *Holarctic Ecology* 4:155-160.

Beaudoin, C.P. 1998. Stable isotope study of food webs in lakes of Alberta's boreal forest. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Gessner, M.O., Schieferstein, B., Muller, U., Barkmann, S. & Lenfers, U.A. 1996. A partial budget of primary organic carbon flows in the littoral zone of a hardwater lake. *Aquat. Bot.* 55:93-105.

Jenkerson, C.G. & Hickman, M. 1986. Interrelationships among the epipelon, epiphyton and phytoplankton in a eutrophic lake. *Int. Revue Ges. Hydrobiol.* 71(4):557-79.

Jones, R.C. 1984. Application of a primary production model to epiphytic algae in a shallow, eutrophic lake. *Ecology* 65: 1895-1903.

Kairesalo, T. 1980. Comparison of in situ photosynthetic activity of epiphytic, epipelic and planktonic algal communities in an oligotrophic lake, southern Finland. *J. Phycol.* 16:57-62.

Lamberti, G.A., Ashkenas, L.R., Gregory, S.V. & Steinman, A.D. 1987. Effects of three herbivores on periphyton communities in laboratory streams. *J. N. Am. Benth. Soc.* 6:92-104.

Phillips, G.L., Eminson, D. & Moss, B. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4:203-126.

Raspopov, I.M., Andronikova, I.N., Dotsenko, O.N., Kurashov, E.A., Letanskaya, G.I., Panov, V.E., Rychkova, M.A., Telesh, I.V., Tchernykh, O.A. & Vorontsov, F.F. 1996. Littoral zone of Lake Ladoga: ecological state evaluation. *Hydrobiologia* 322: 39-47.

Sondergaard, M. & Sand-Jensen, K. 1978. Total autotrophic production in oligotrophic, Lake Kalgaard, Denmark. *Verh. Internat. Verein. Limnol.* 20: 667-673.

Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. *Verh. Internat. Verein. Limnol.* 24:6-24.

Appendix A: Estimation of macrophyte biomass and surface area.

A.0 Estimation of macrophyte biomass

Estimates of macrophyte biomass (grams dry weight · m^{-2} lake surface area) were obtained in three of the four lakes (SPH 20, SPH 200 and SPH 800) in August 1998 (K. Wolfstein, unpublished data). Five or six transects were sampled in each lake at three stations (1, 2 and 3 m depth). Macrophyte samples were sorted by species and dried until a constant weight was obtained. Percent of surface irradiance at 0.25 m intervals was measured near the point of maximum depth of each lake with a LiCor spherical quantum sensor (Model LI-193SA). In each lake, mean biomass of each submergent macrophyte species were plotted against percent surface irradiance at 1, 2 and 3 m depth. Resulting regression equations were used to predict the biomass of each macrophyte species at 0.5, 1.5 and 2.5 m depth from measurements of percent surface irradiance.

Due to the remote location of SPH 100, logistic constraints did not allow for a direct measurement of macrophyte biomass. However, visual estimates suggested that macrophyte species composition and distribution were similar to that of SPH 800. Therefore, regression equations used to predict the biomass of each macrophyte species in SPH 800 were combined with measurements of percent surface irradiance from SPH 100 made at 0.5 and 1.5 depth.

A.1 Estimation of macrophyte surface area

Estimates of macrophyte biomass were converted into available surface area (m^2) per m^2 of lake surface area with equations relating colorimetrically measured surface area (Cattaneo and Kalff 1982) to dry weight (Chapter Two). Since Chambers and Prepas (1990) suggest that macrophyte biomass increased 3 times between June and August in Long Lake, Alberta, estimates of available surface area for August from this study were

converted into seasonal estimates based on a three fold increase in biomass between June and August. Macrophyte surface area was assumed to begin declining in September. Resulting estimates of macrophyte surface area (m^2 surface area$\cdot m^{-2}$ of littoral zone) were then multiplied by the rate of epiphyton photosynthesis per m^2 of macrophyte substrata to provide an estimate of epiphyton photosynthesis comparable to rates of phytoplankton photosynthesis.

Appendix B: Epiphyton photosynthesis-irradiance curves.

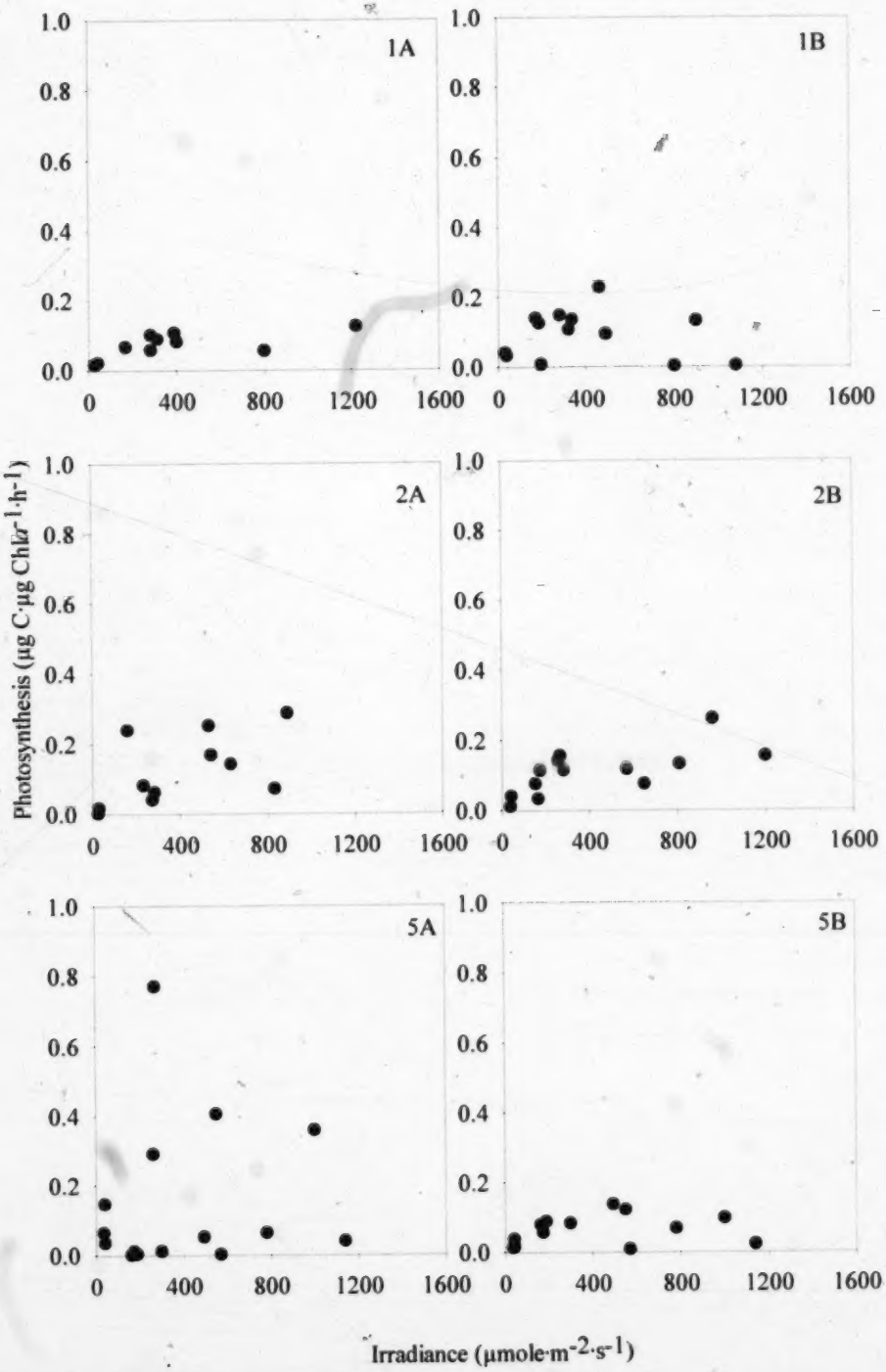


Figure B1: Epiphyton photosynthesis-irradiance curves in SPH 20 (June 1998).

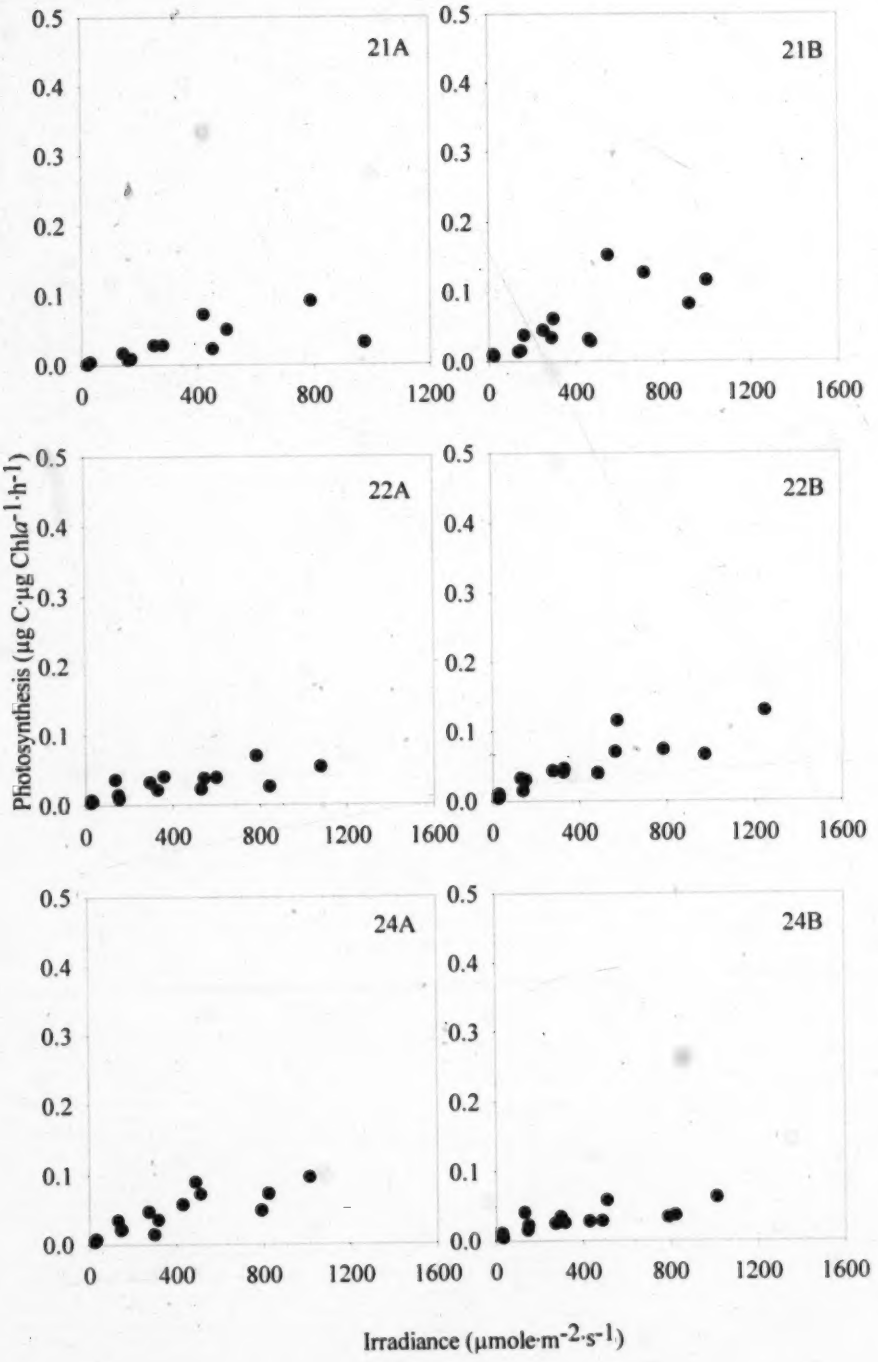


Figure B2: Epiphyton photosynthesis-irradiance curves in SPH 100 (June 1998).

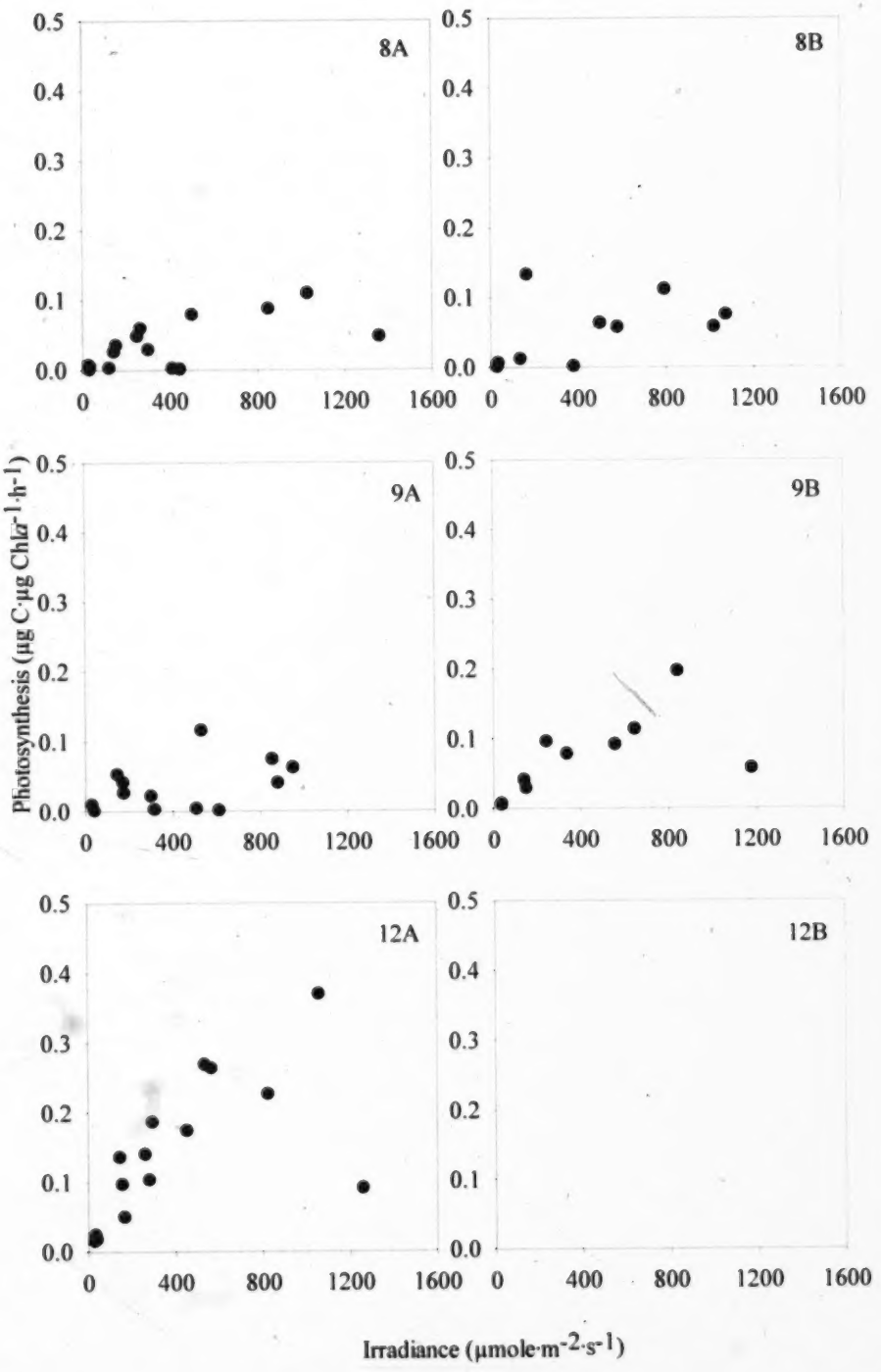


Figure B3: Epiphyton photosynthesis-irradiance curves in SPH 200 (June 1998).

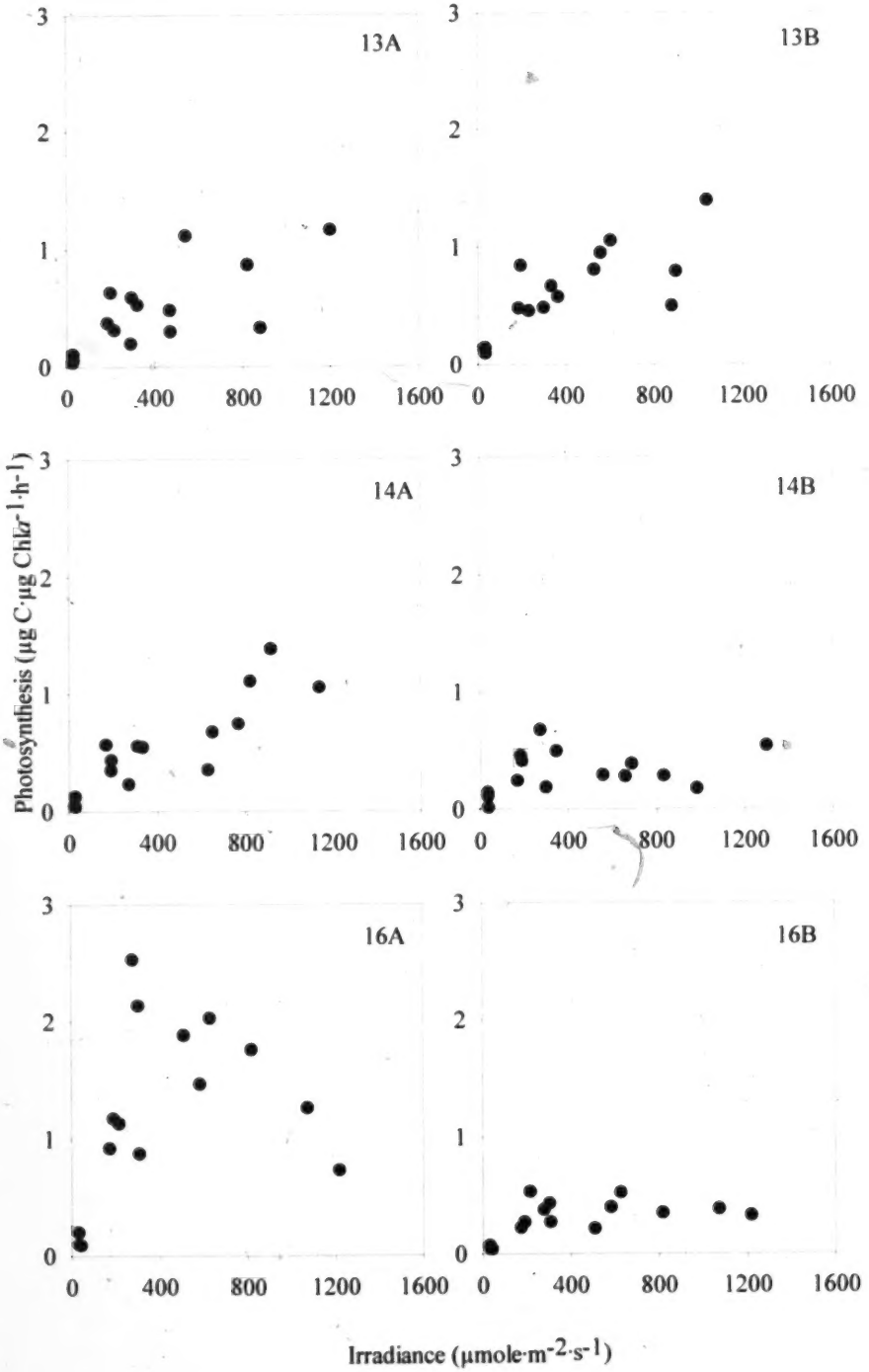


Figure B4: Epiphyton photosynthesis-irradiance curves in SPH 800 (June 1998).

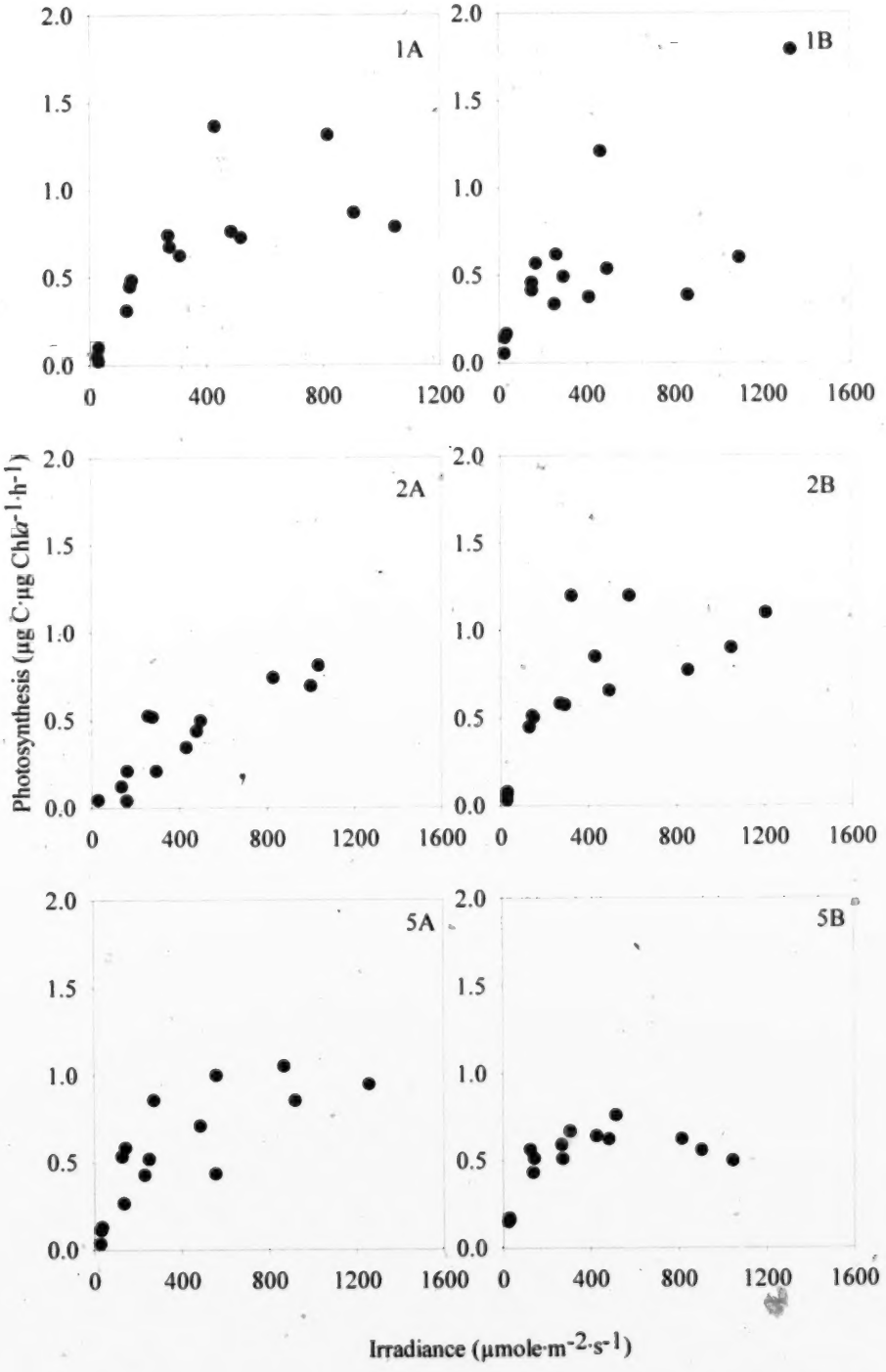


Figure B5: Epiphyton photosynthesis-irradiance curves in SPH 20 (July 1998).

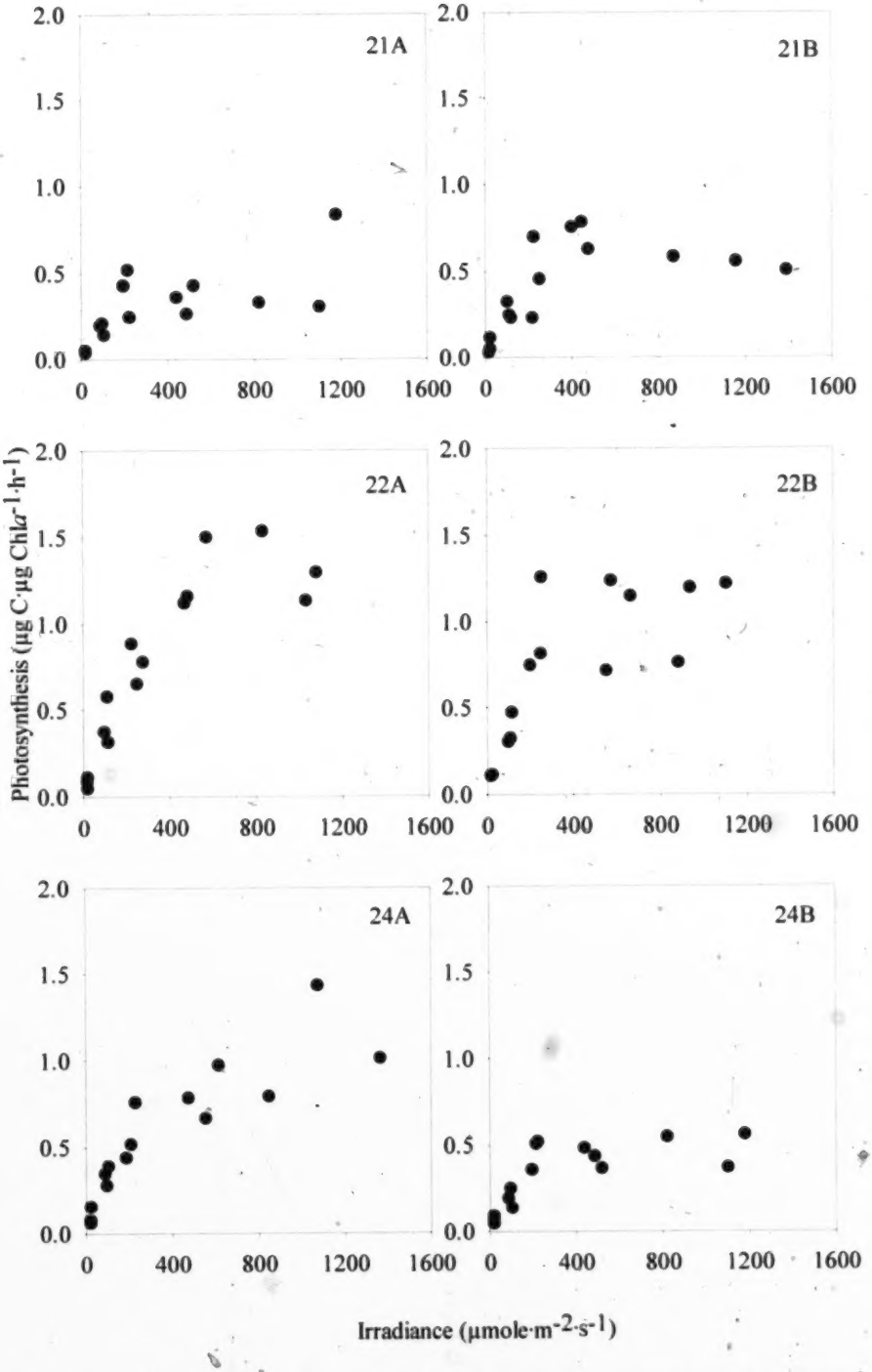


Figure B6: Epiphyton photosynthesis-irradiance curves in SPH 100 (July 1998).

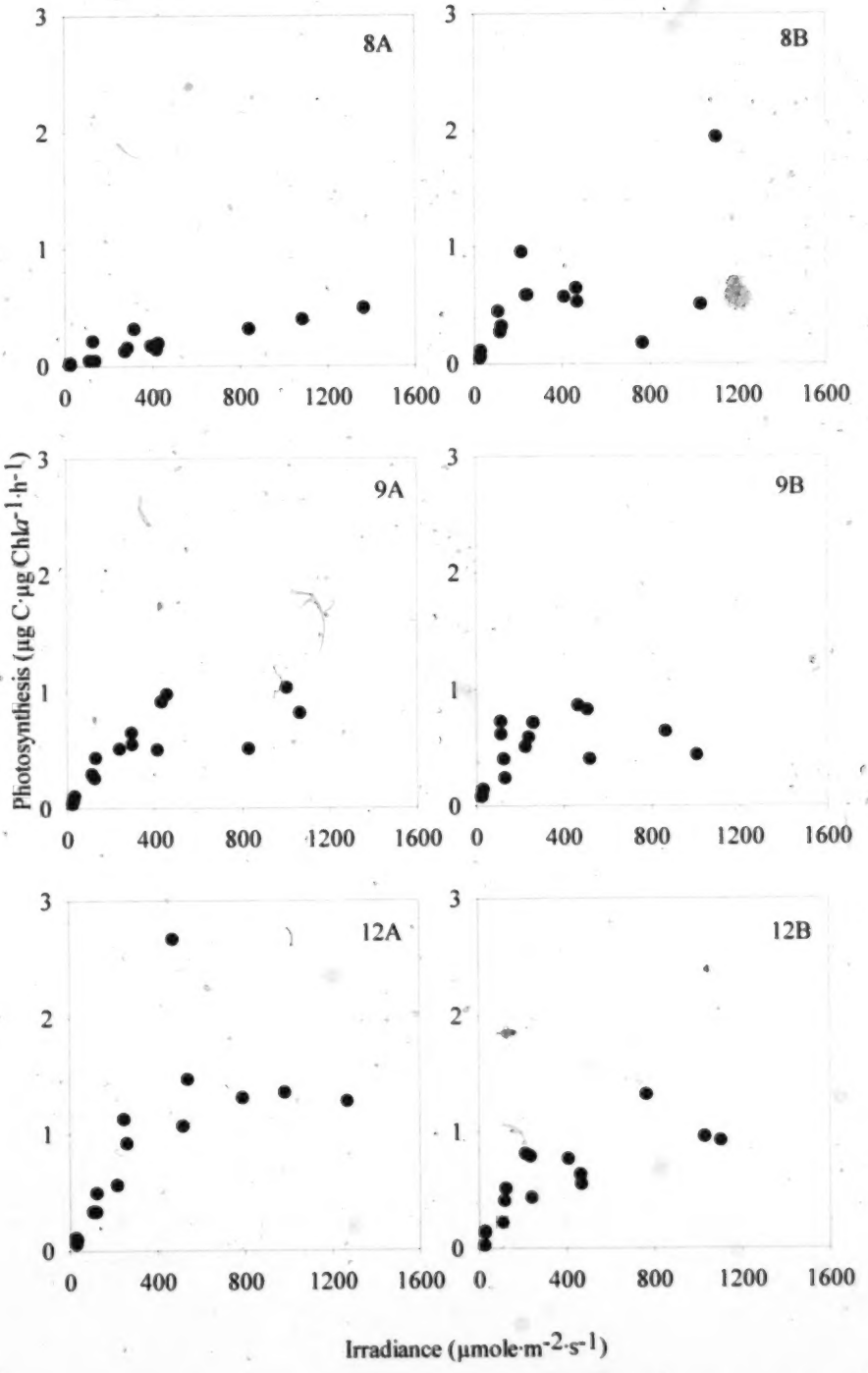


Figure B7: Epiphyton photosynthesis-irradiance curves in SPH 200 (July 1998).

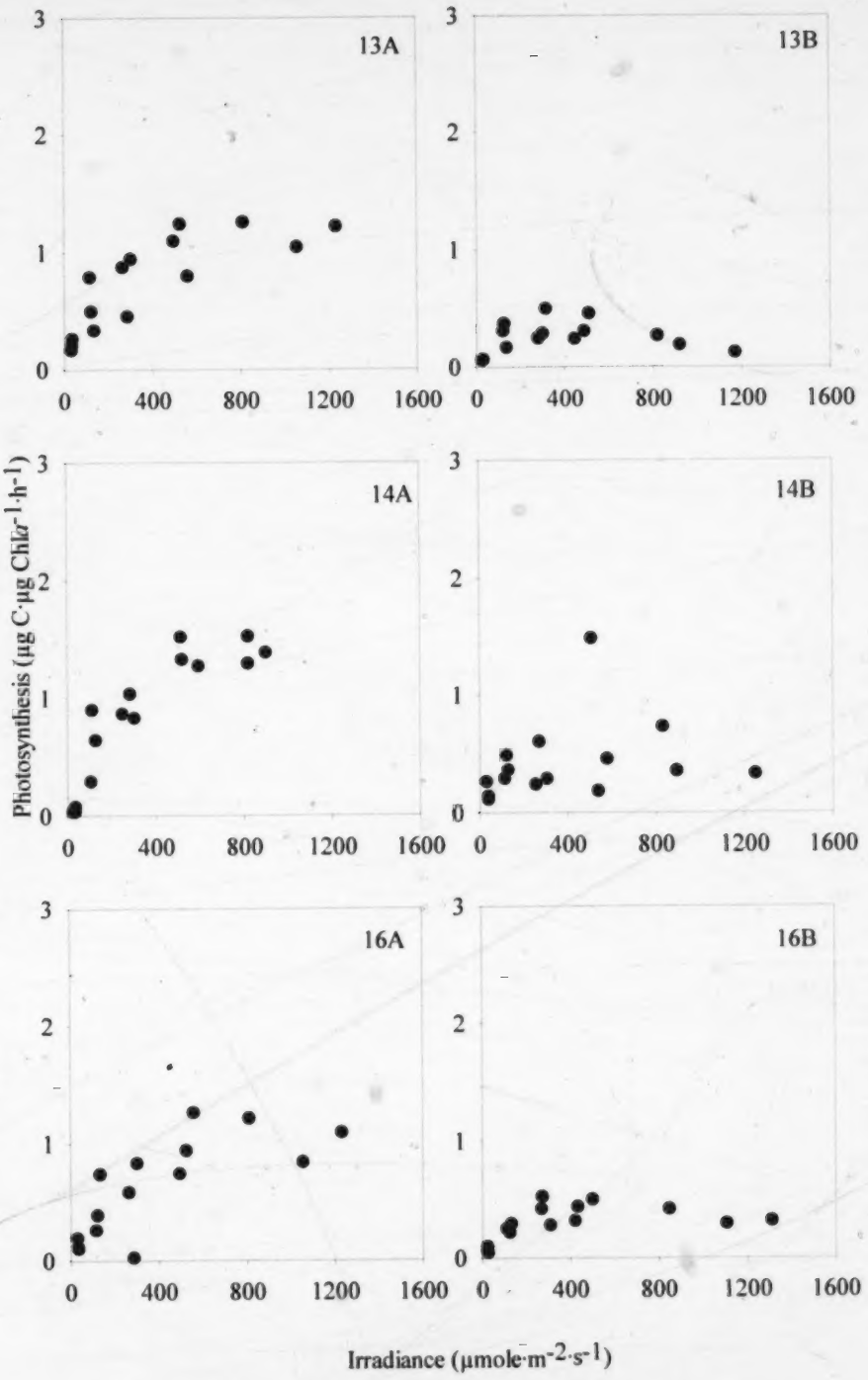


Figure B8: Epiphyton photosynthesis-irradiance curves in SPH 800 (July 1998).

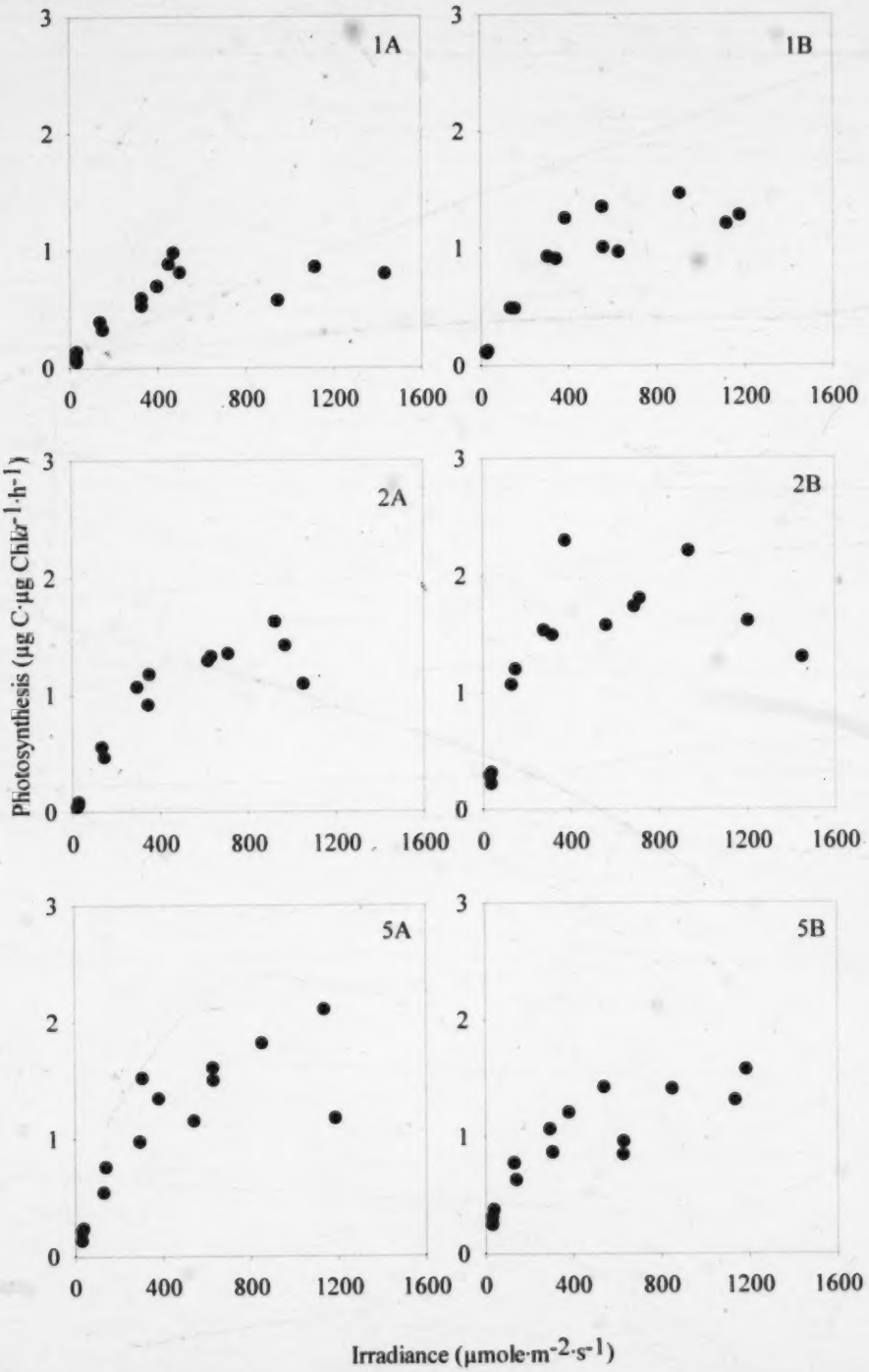


Figure B9: Epiphyton photosynthesis-irradiance curves in SPH 20 (August 1998).

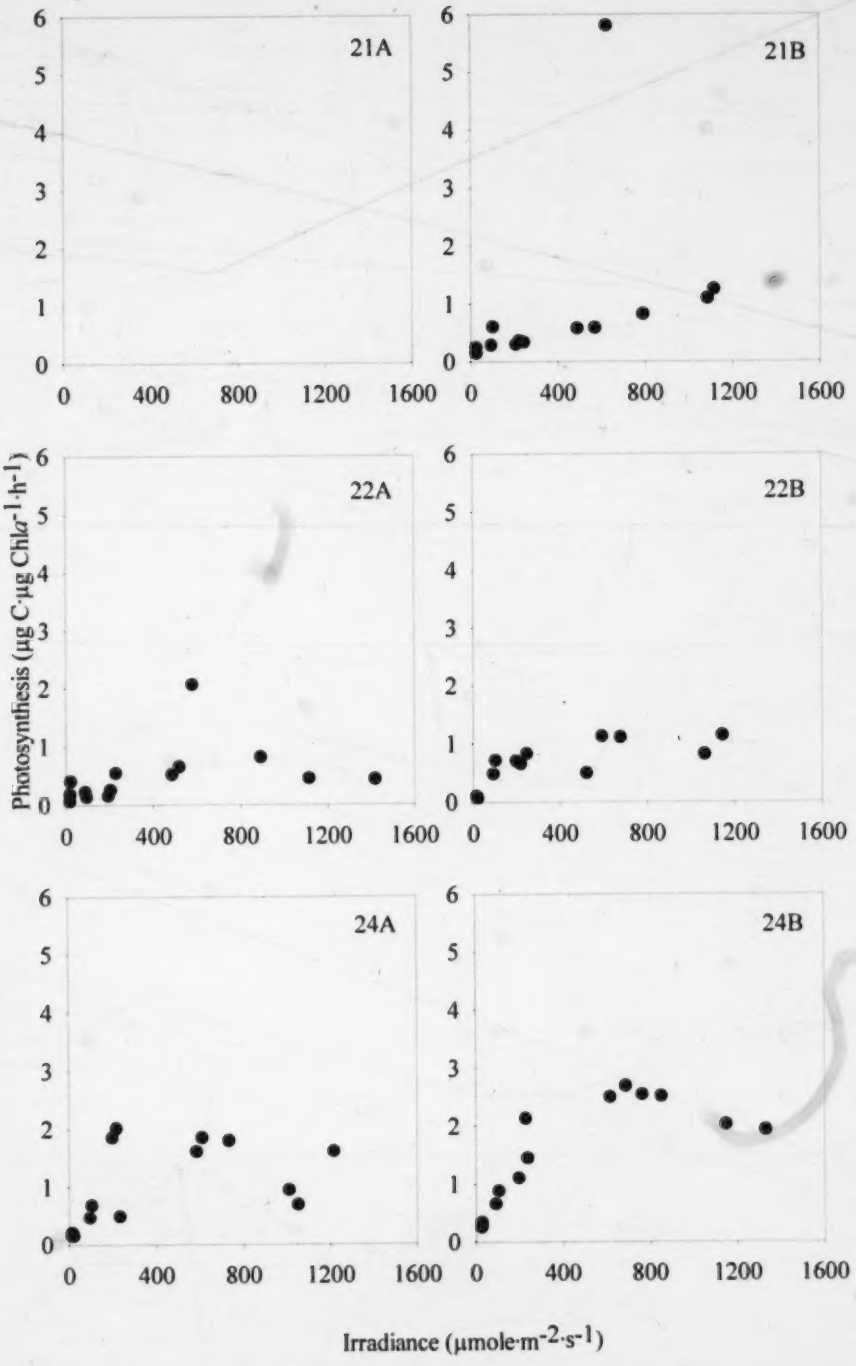


Figure B10: Epiphyton photosynthesis-irradiance curves in SPH 100 (August 1998).

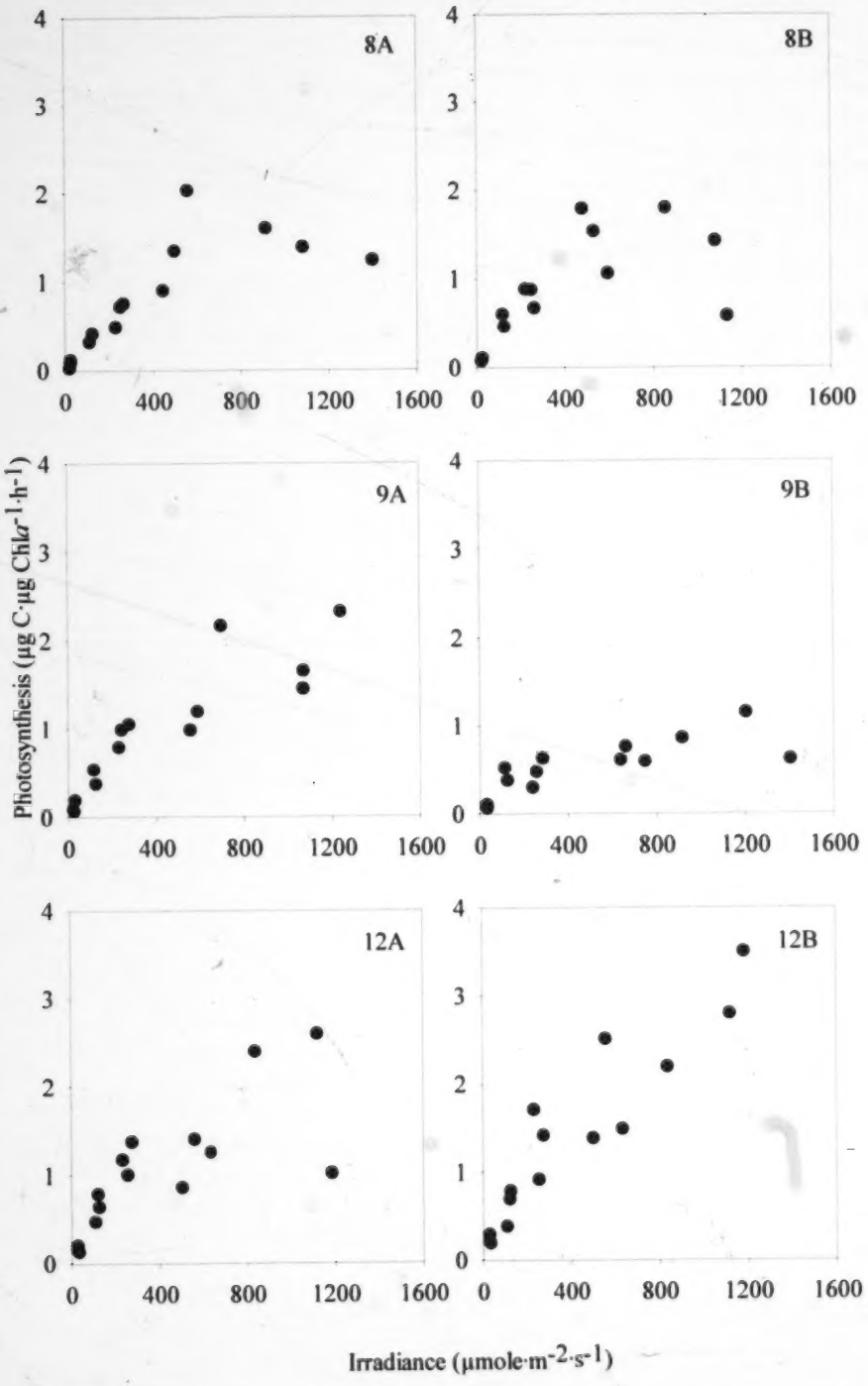


Figure B11: Epiphyton photosynthesis-irradiance curves in SPH 200 (August 1998).

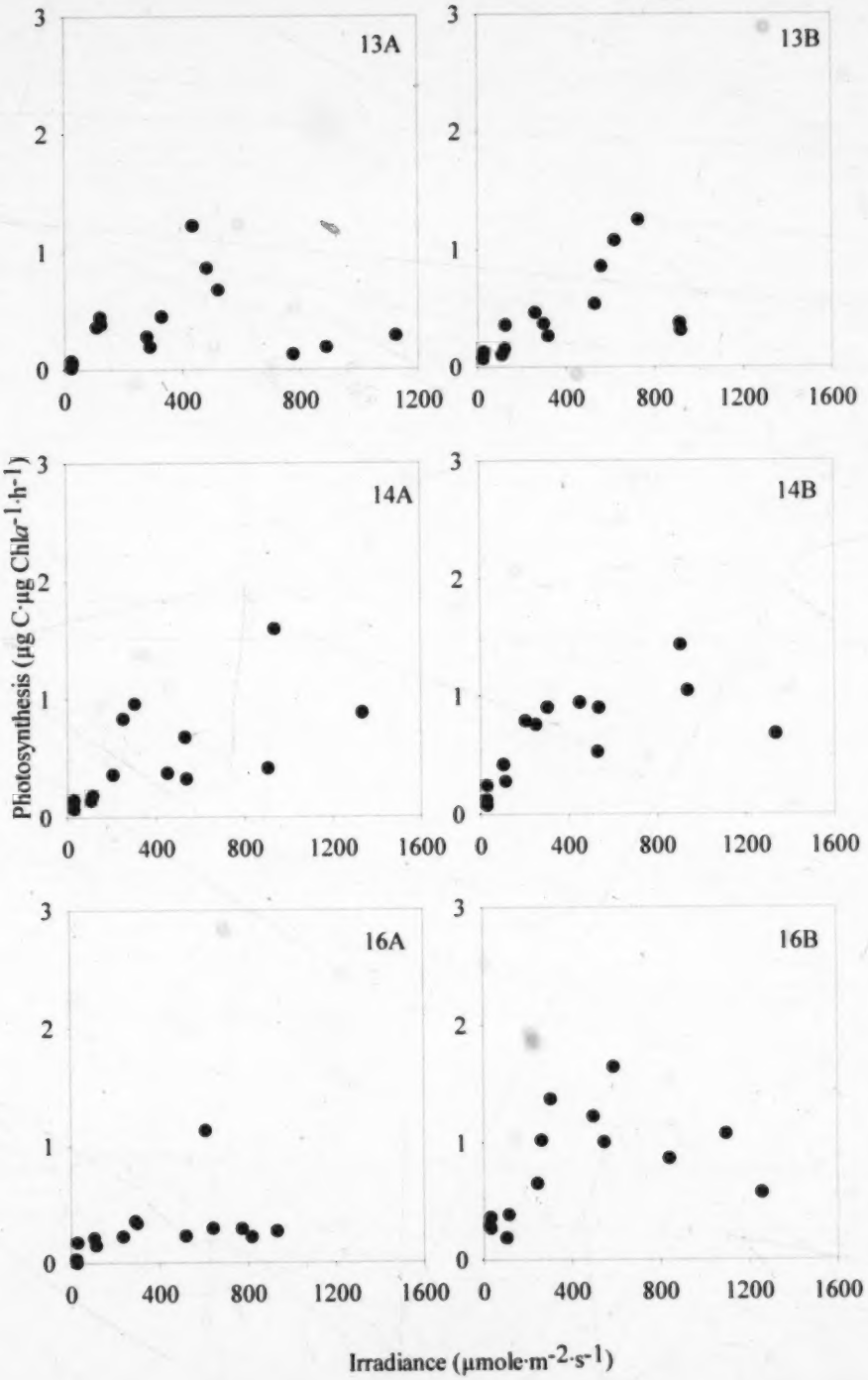


Figure B12: Epiphyton photosynthesis-irradiance curves in SPH 800 (August 1998).

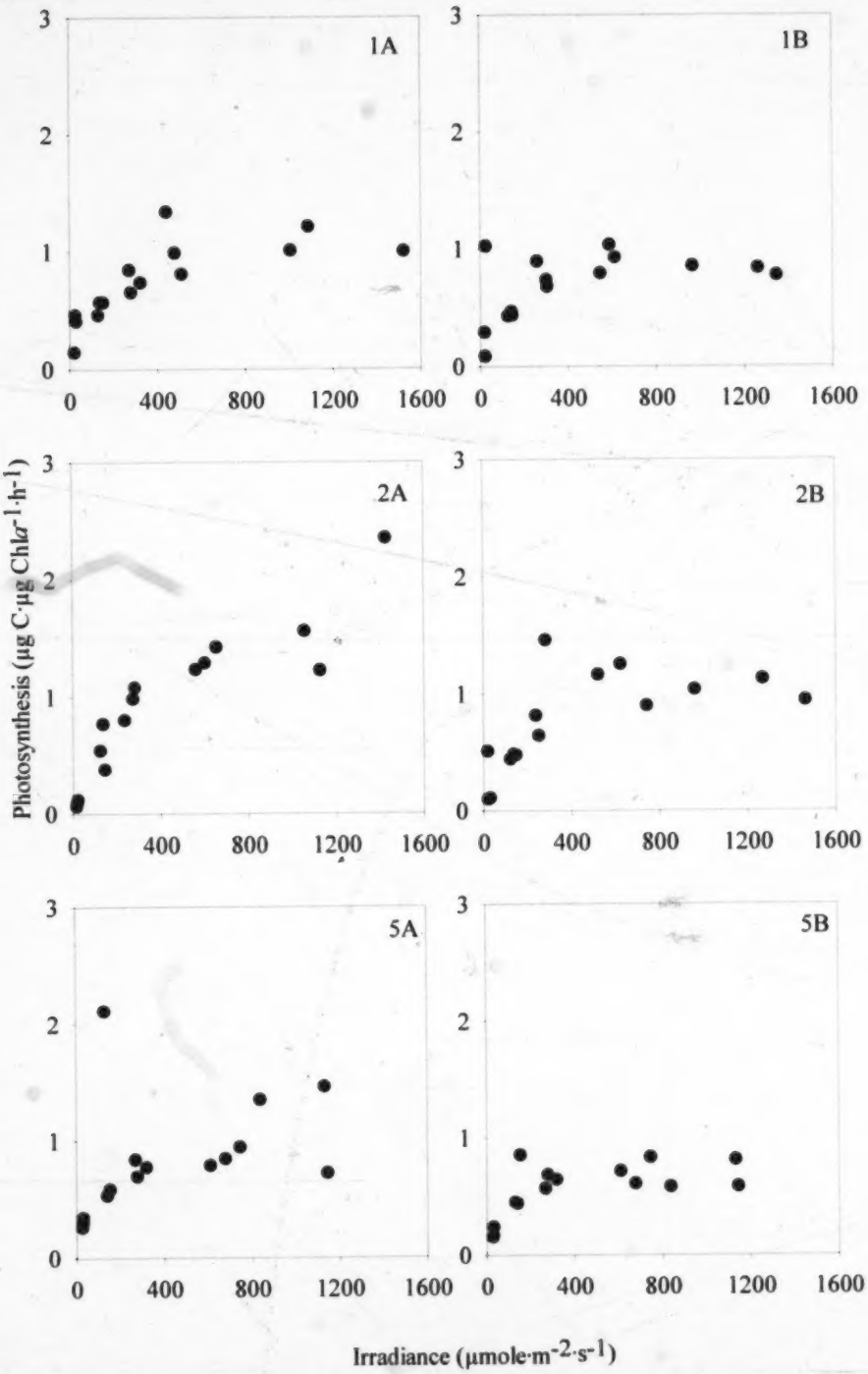


Figure B13: Epiphyton photosynthesis-irradiance curves in SPH 20 (September 1998).

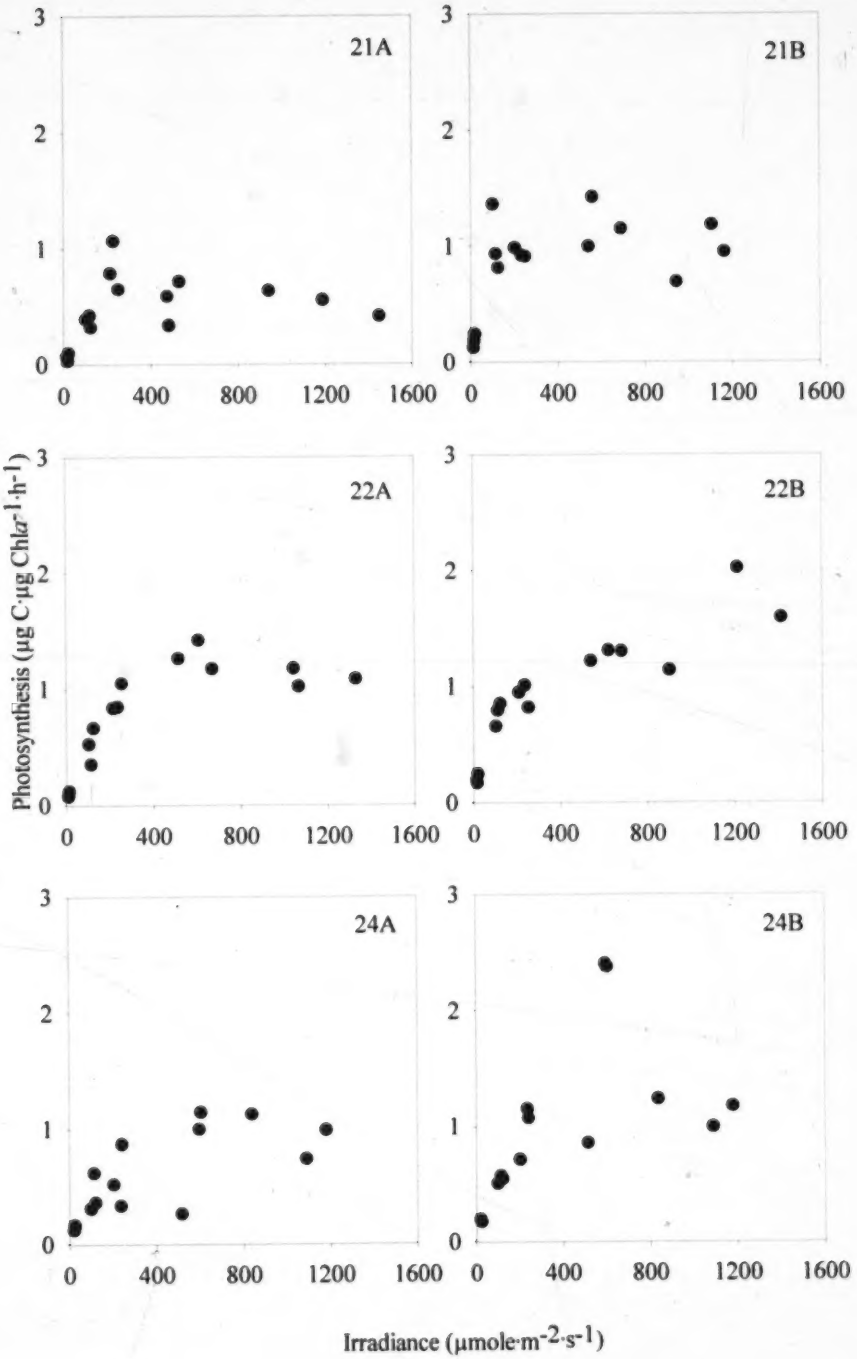


Figure B14: Epiphyton photosynthesis-irradiance curves in SPH 100 (September 1998).

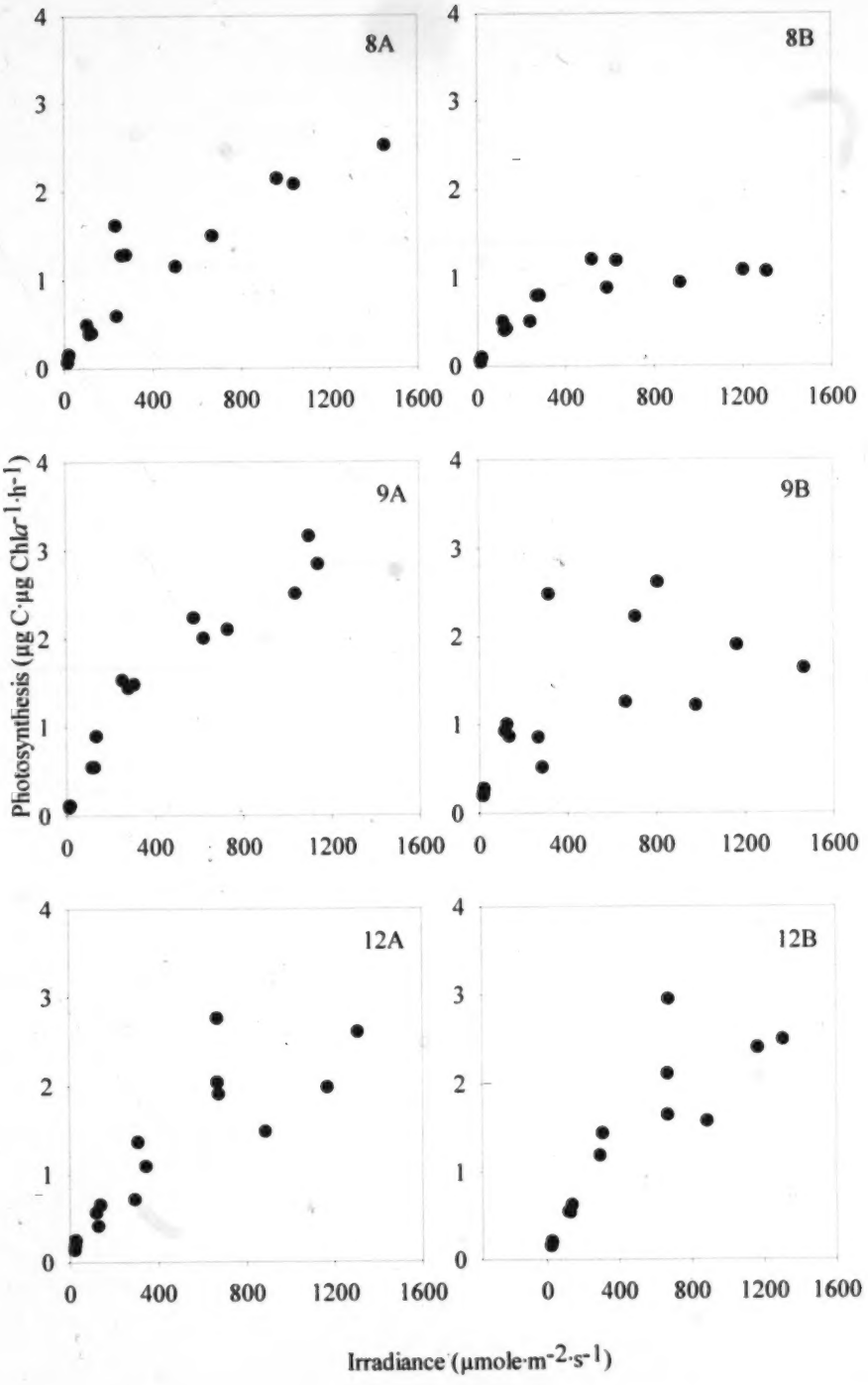


Figure B15: Epiphyton photosynthesis-irradiance curves in SPH 200 (September 1998).

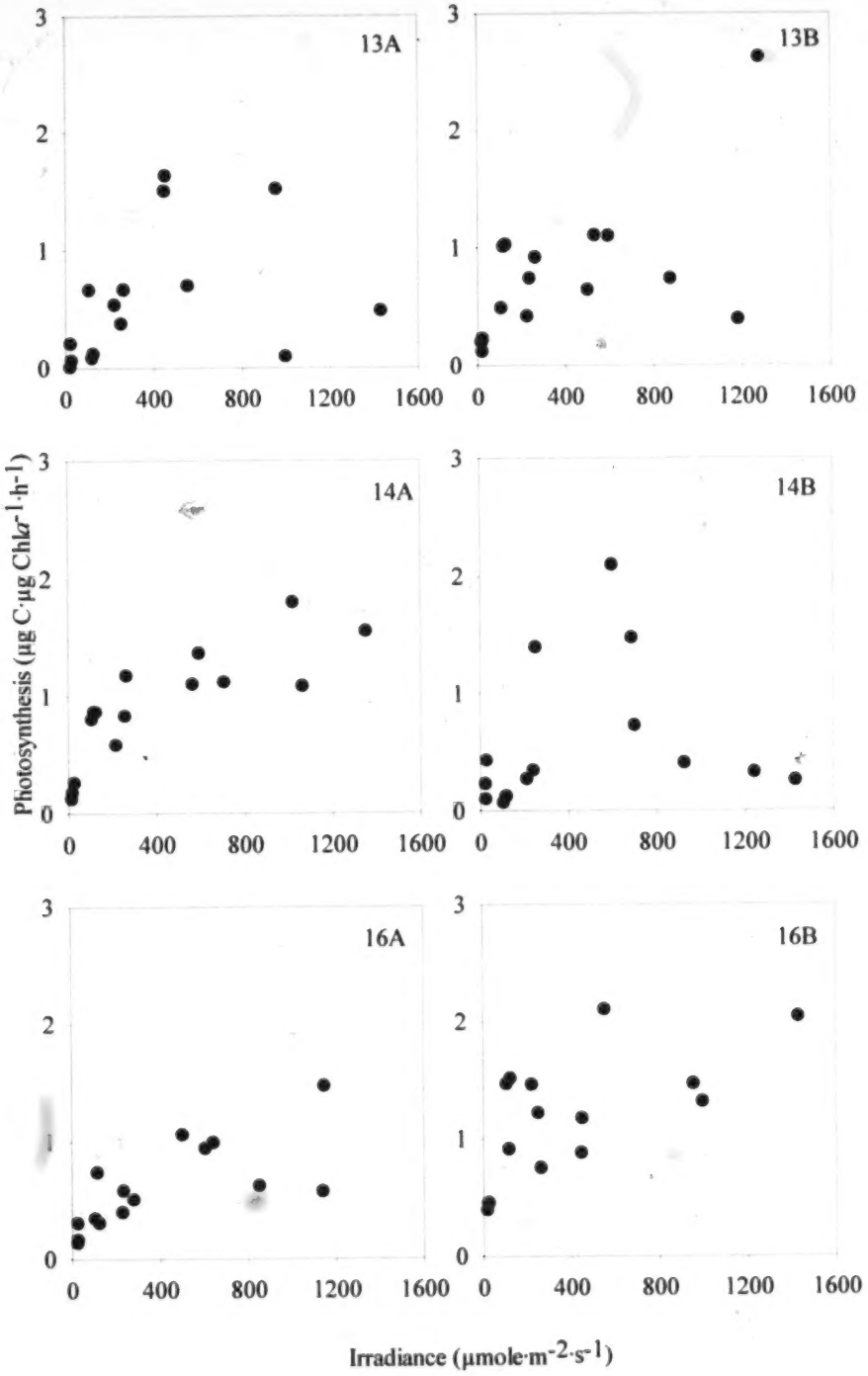


Figure B16: Epiphyton photosynthesis-irradiance curves in SPH 800 (September 1998).

Appendix C: Phytoplankton photosynthesis-irradiance curves.

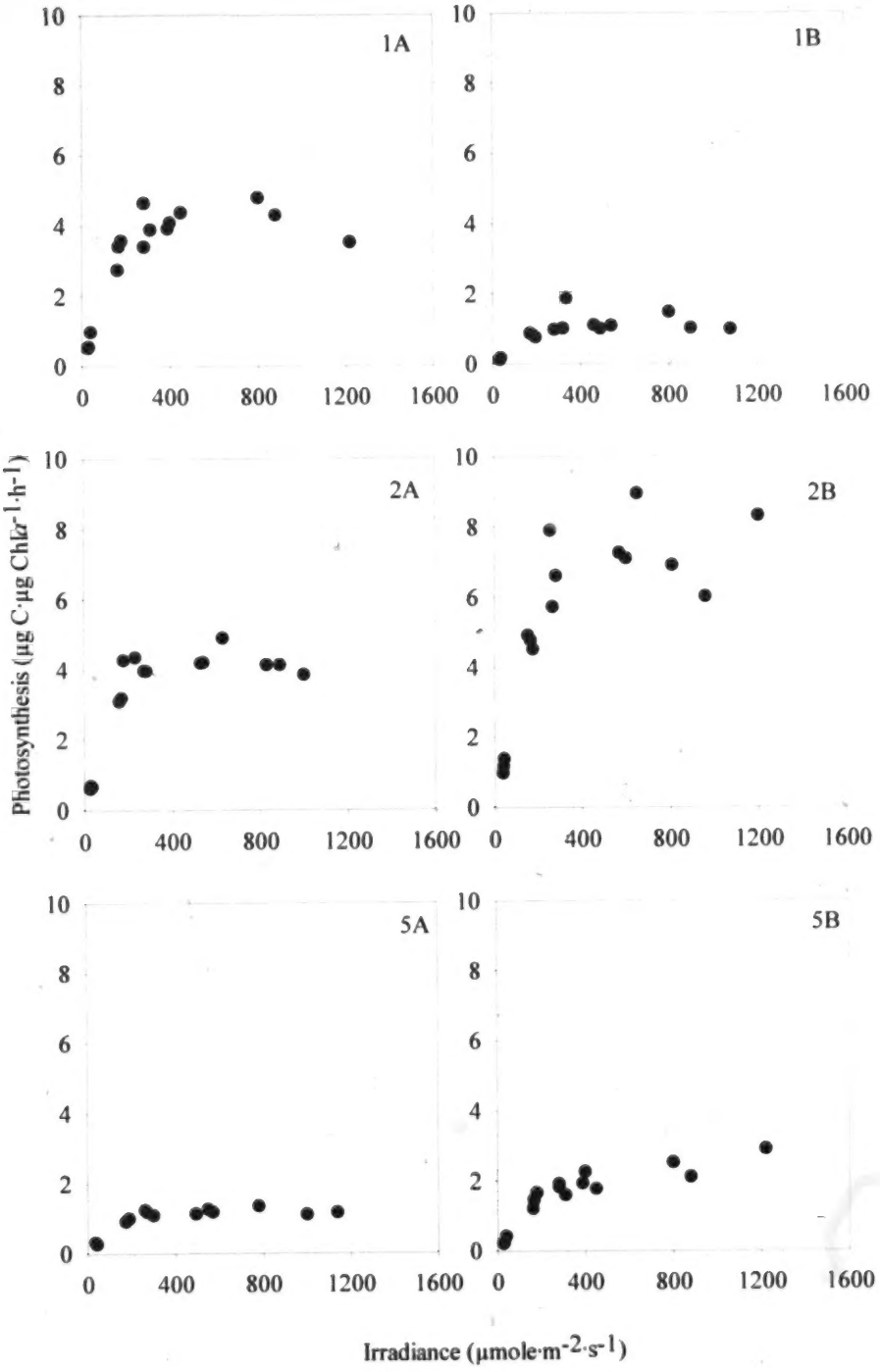


Figure C1: Phytoplankton photosynthesis-irradiance curves in SPH 20 (June 1998).

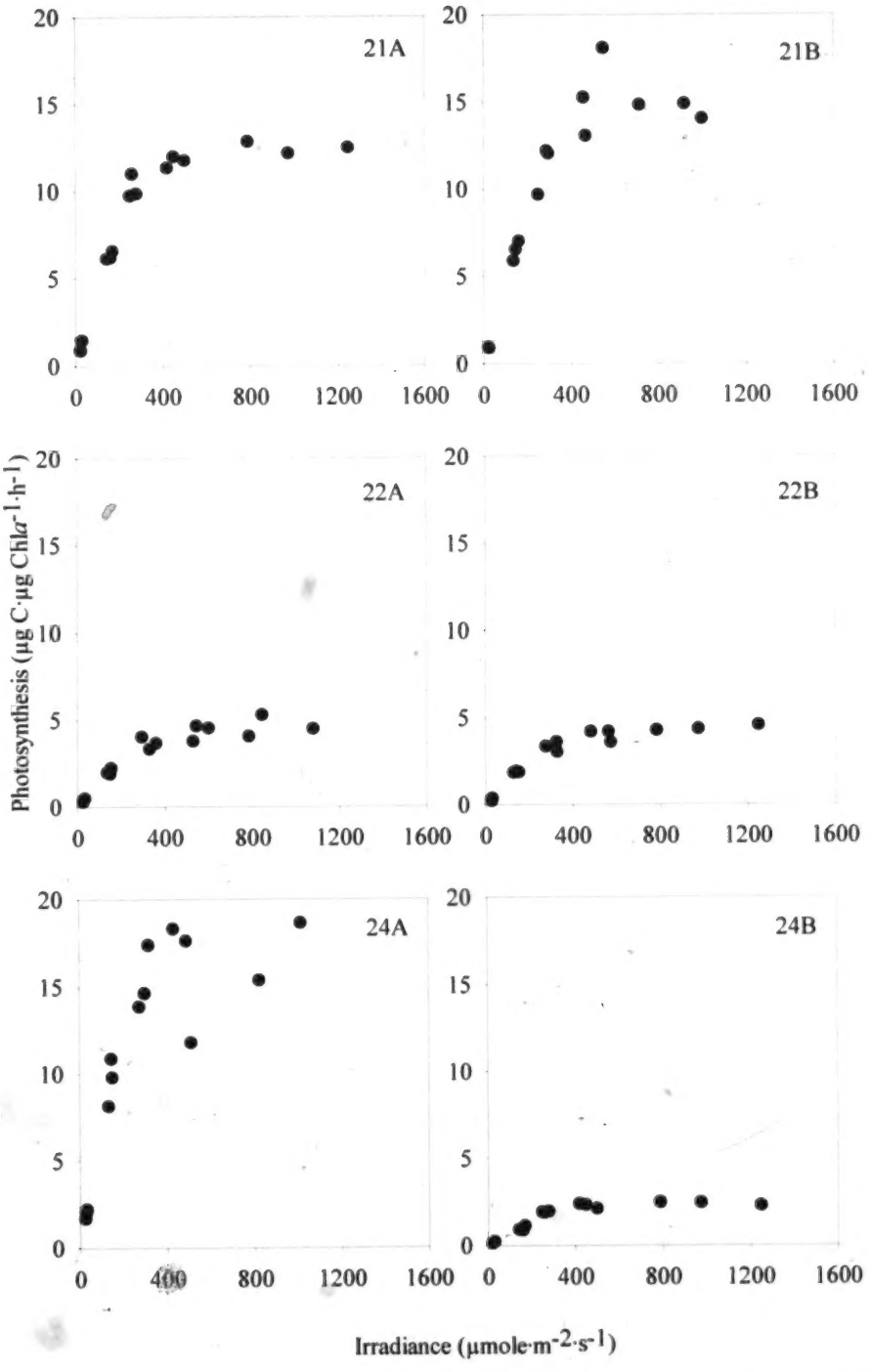


Figure C2: Phytoplankton photosynthesis-irradiance curves in SPH 100 (June 1998).

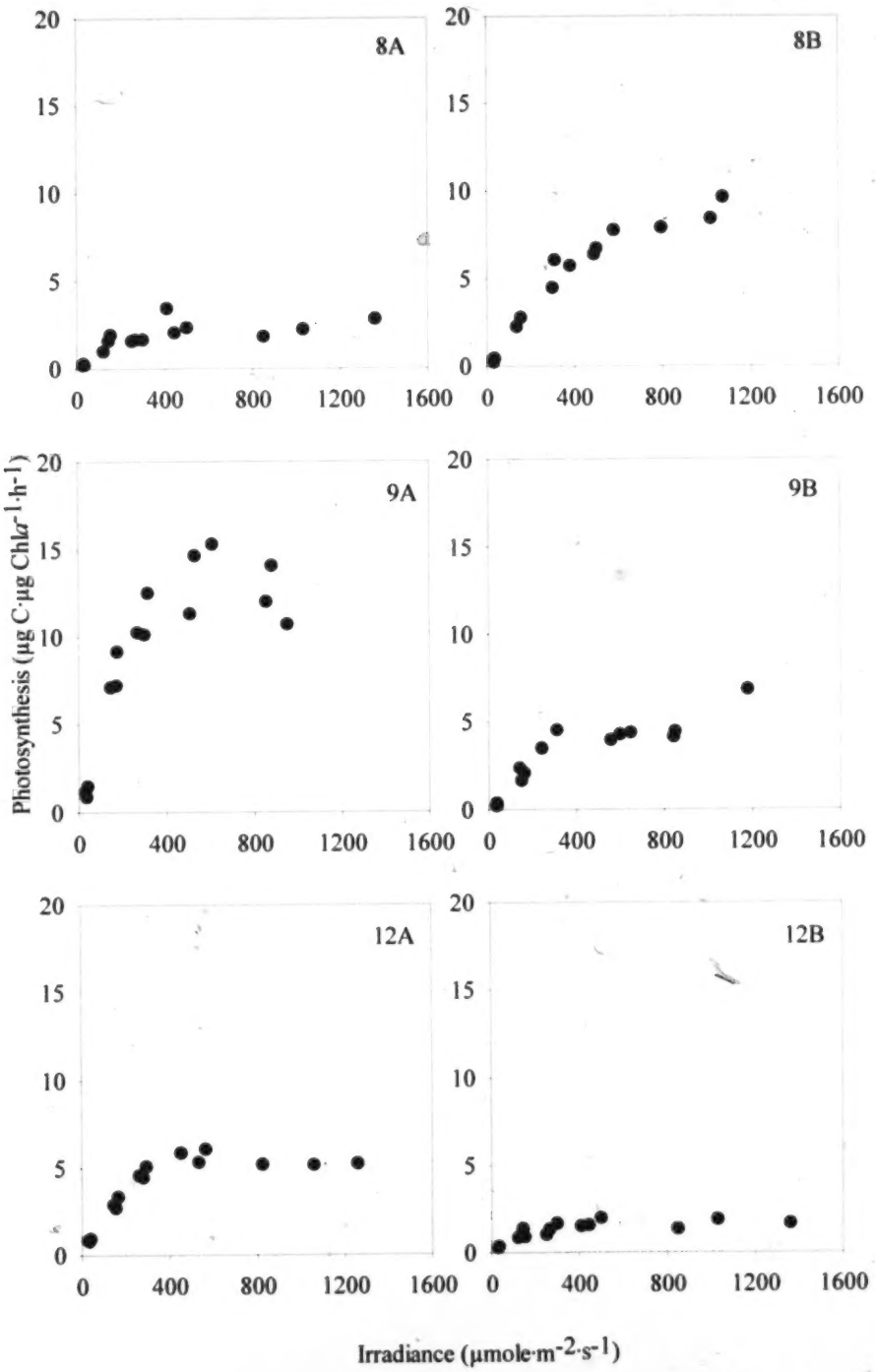


Figure C3: Phytoplankton photosynthesis-irradiance curves in SPH 200 (June 1998).

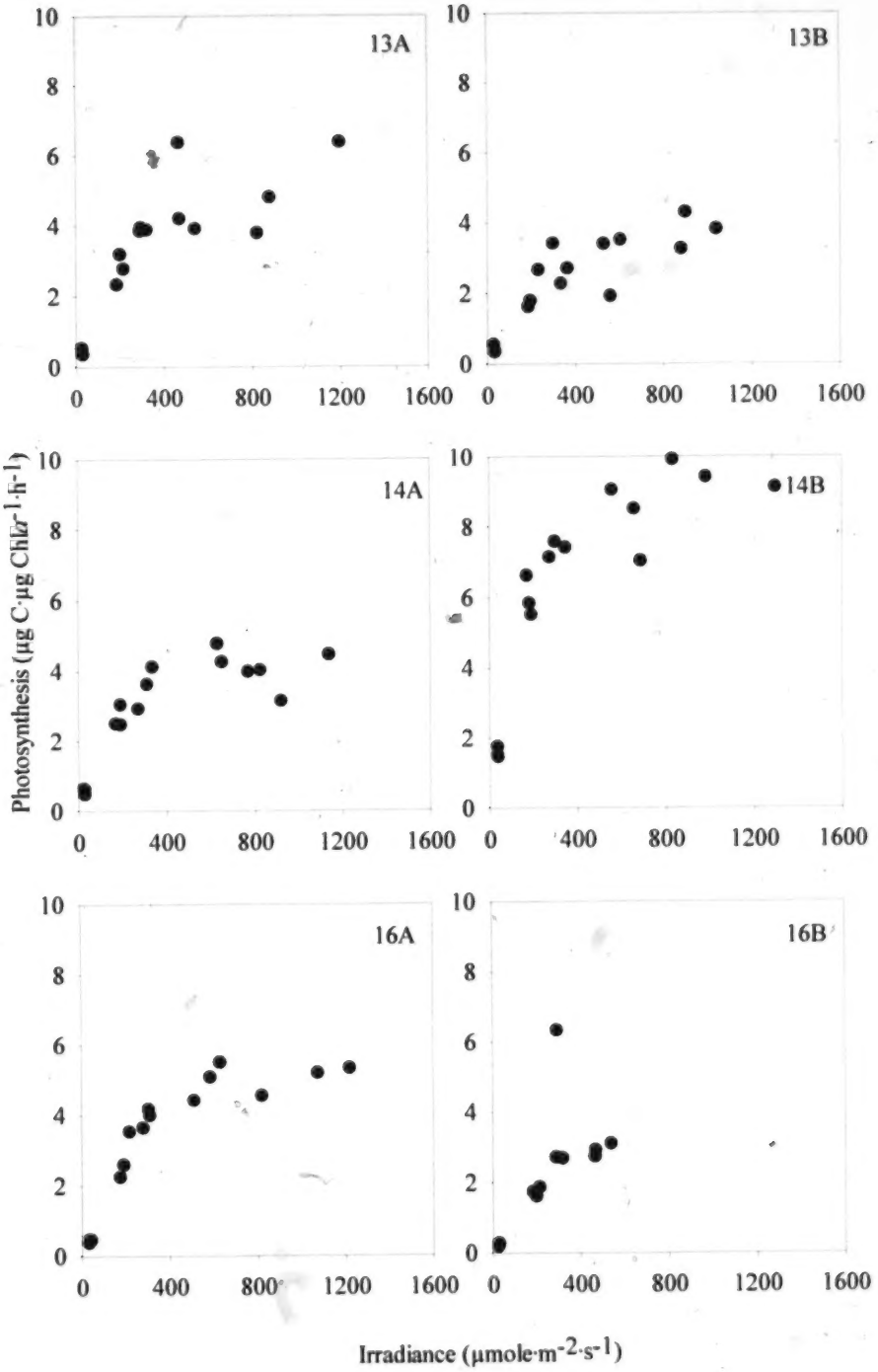


Figure C4: Phytoplankton photosynthesis-irradiance curves in SPH 800 (June 1998).

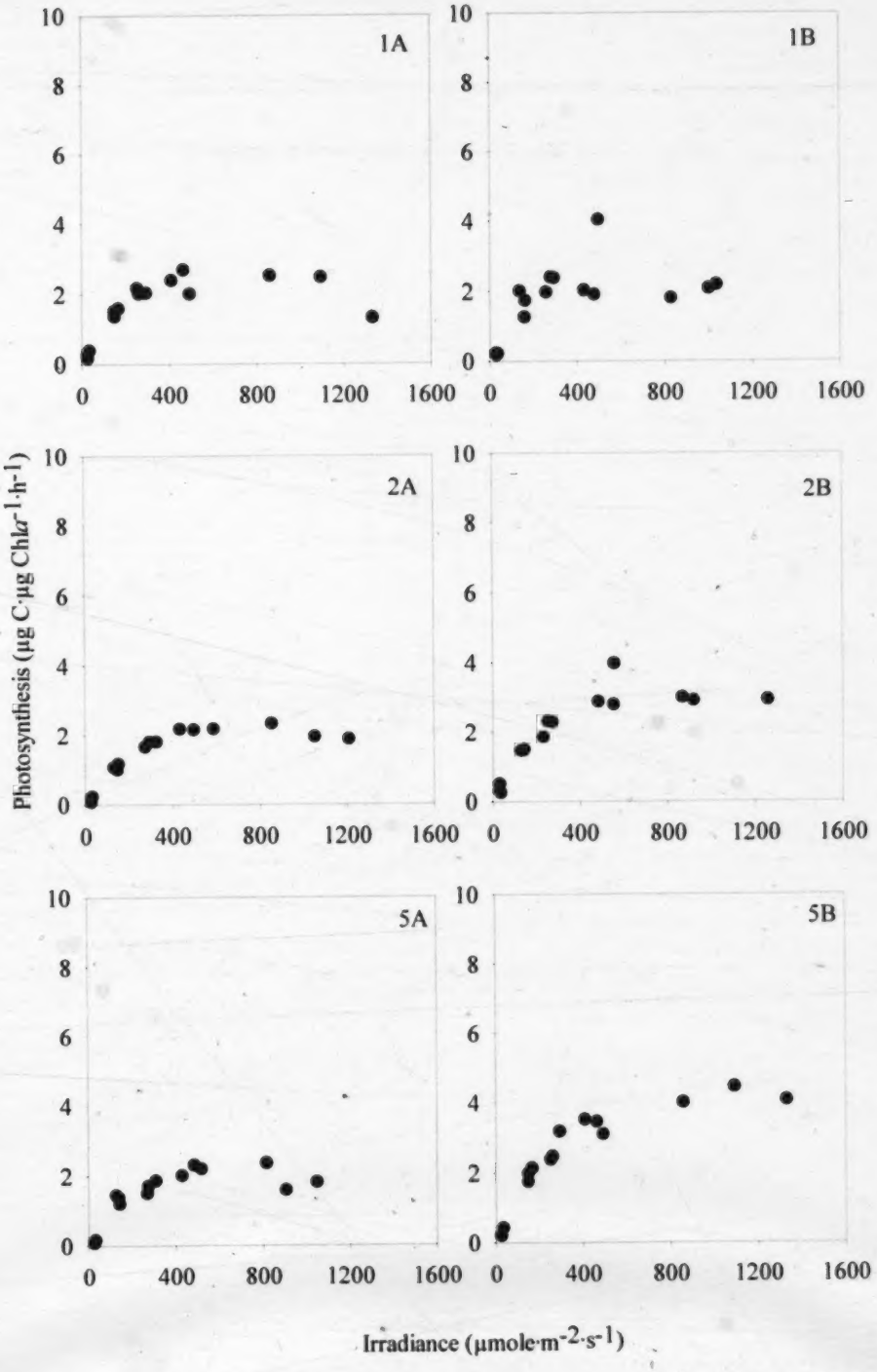


Figure C5: Phytoplankton photosynthesis-irradiance curves in SPH 20 (July 1998).

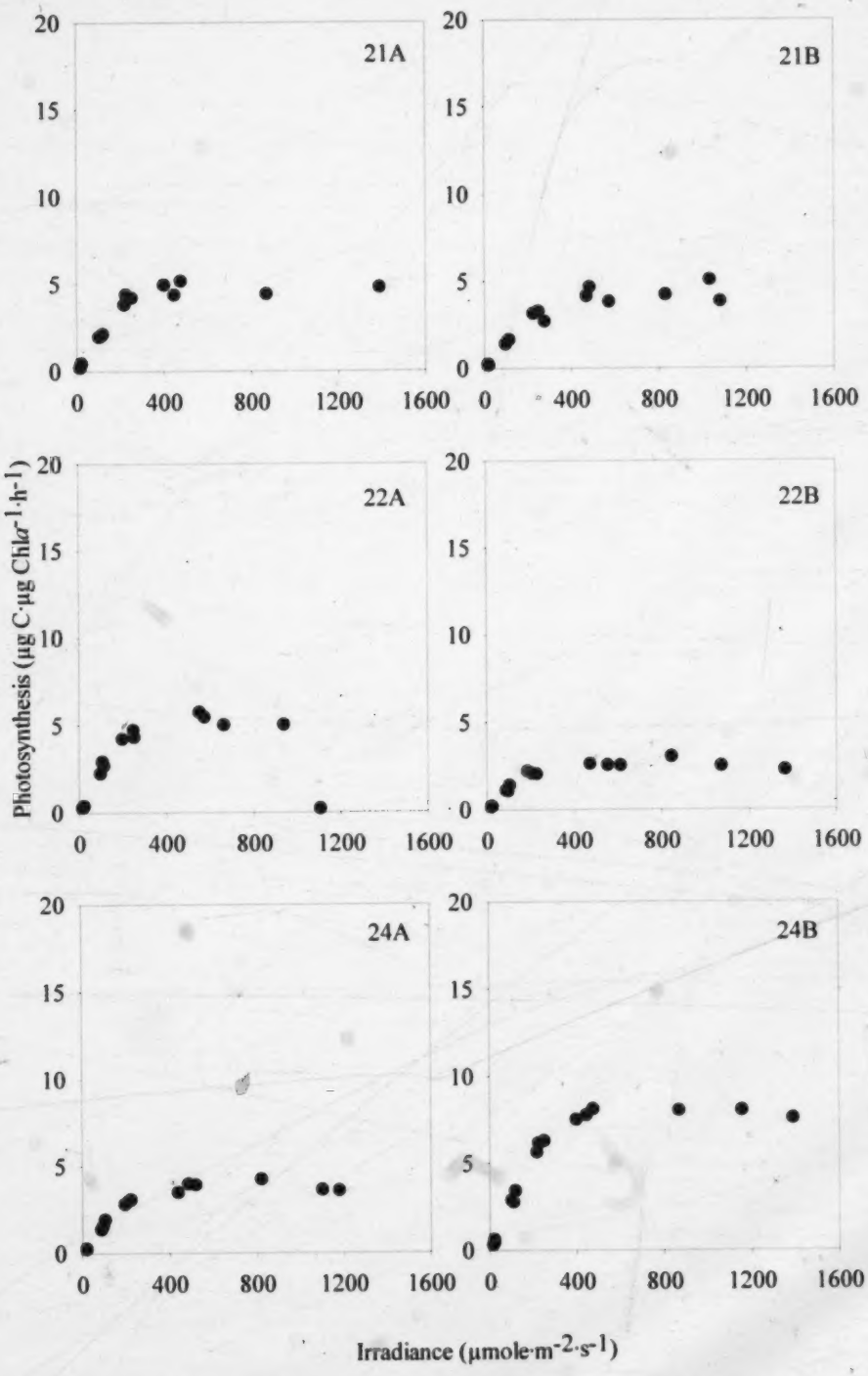


Figure C6: Phytoplankton photosynthesis-irradiance curves in SPH 100 (July 1998).

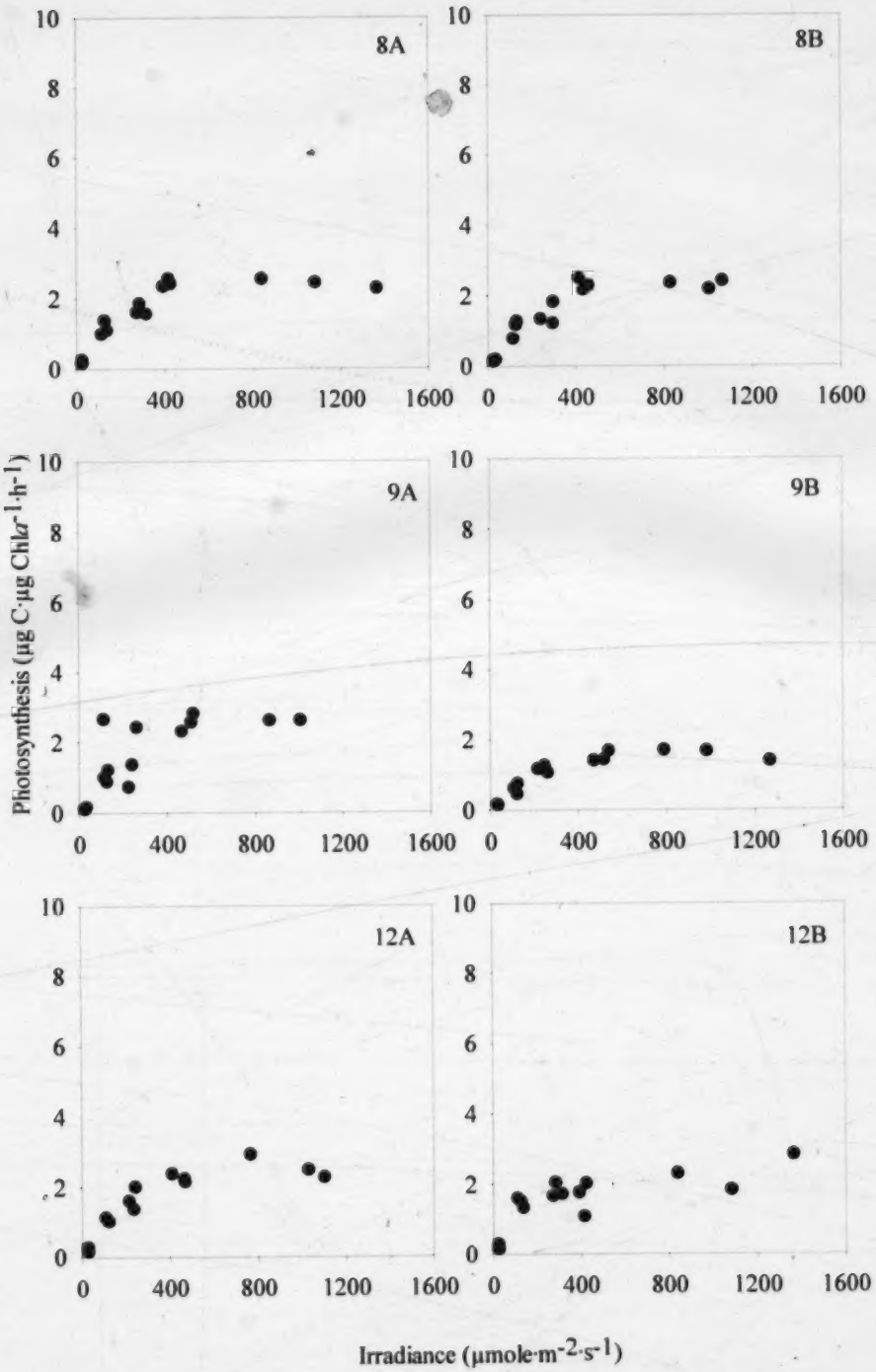


Figure C7: Phytoplankton photosynthesis-irradiance curves in SPH 200 (July 1998).

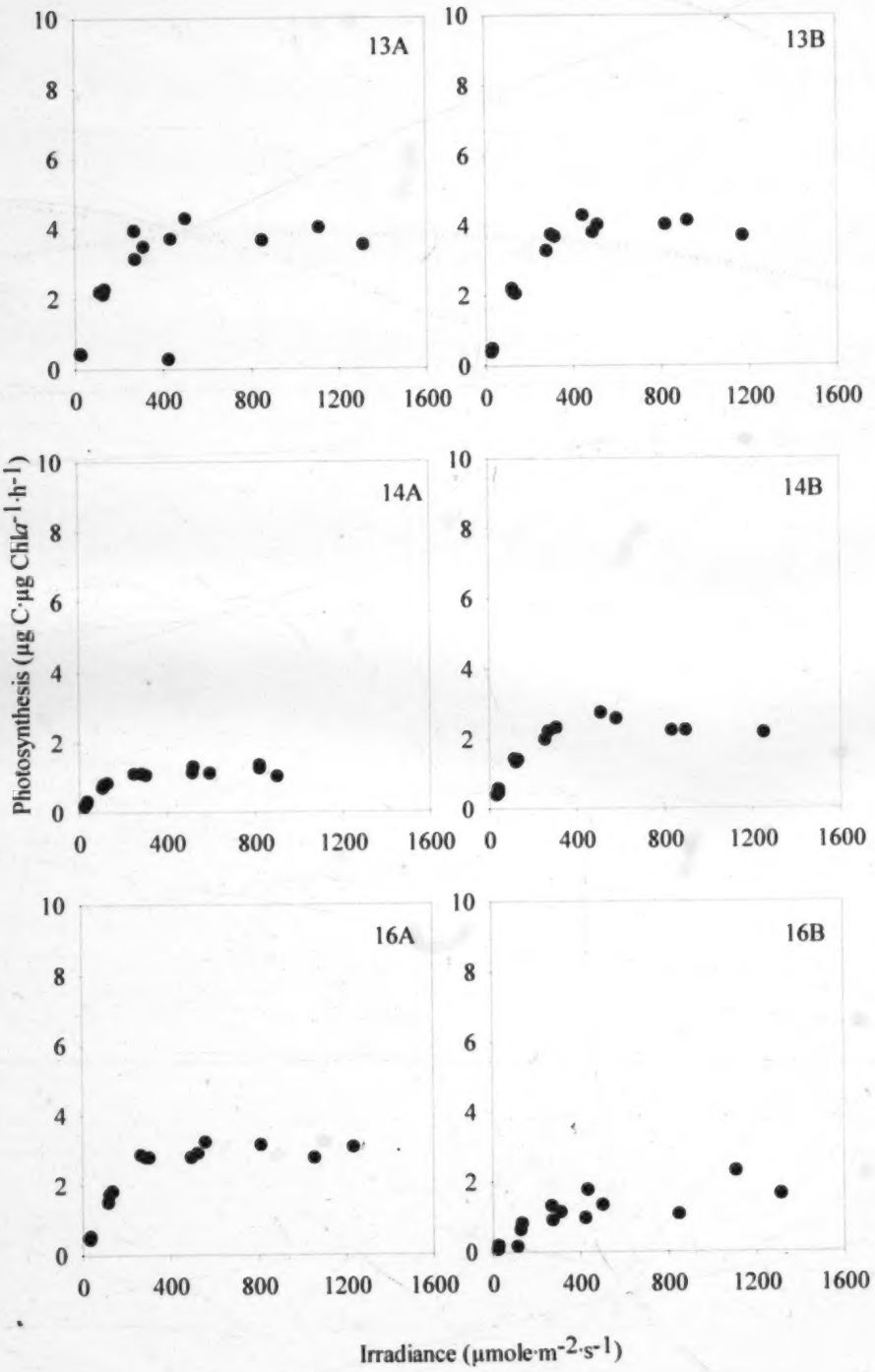


Figure C8: Phytoplankton photosynthesis-irradiance curves in SPH 800 (July 1998).

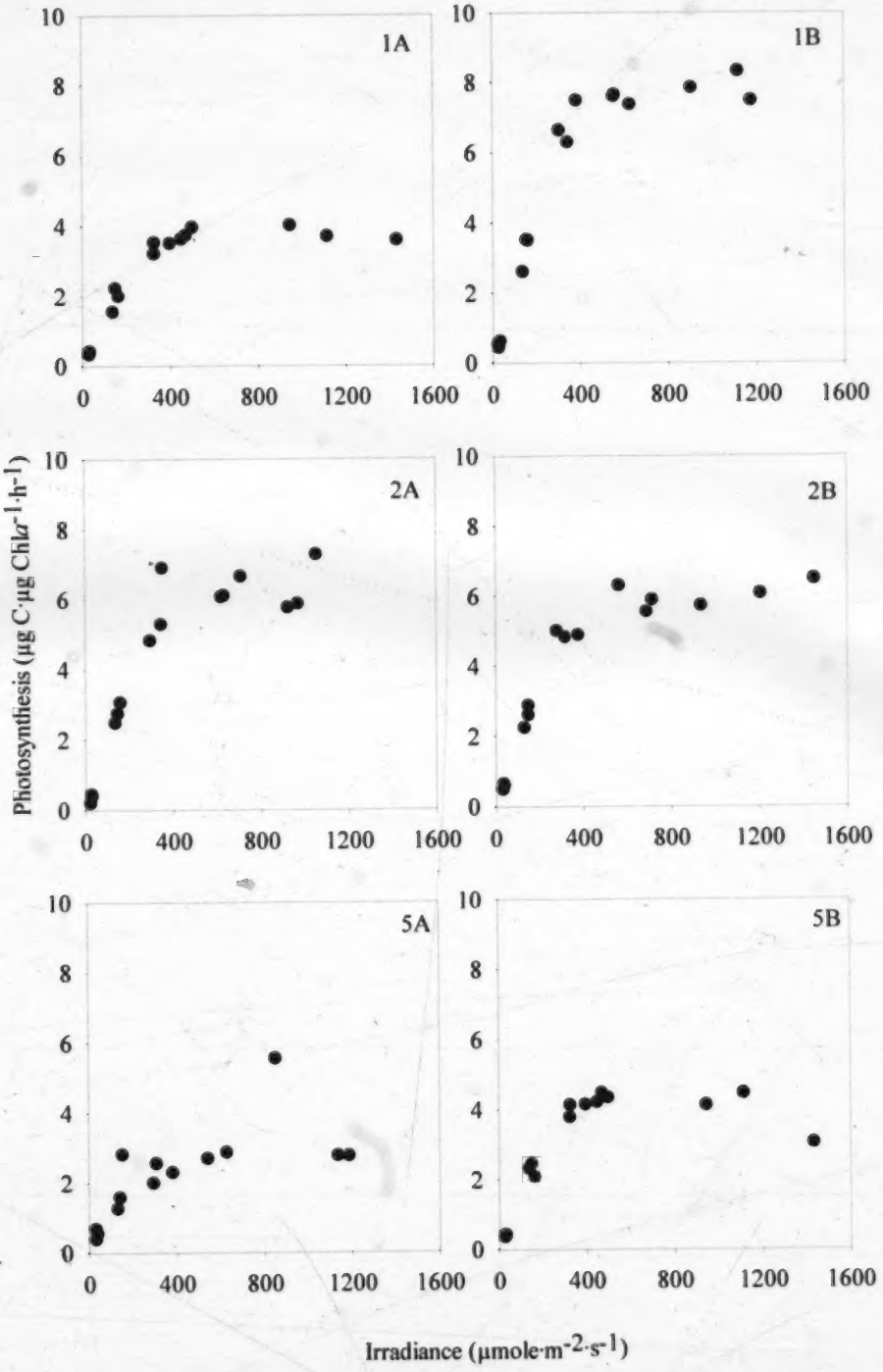


Figure C9: Phytoplankton photosynthesis-irradiance curves in SPH 20 (August 1998).

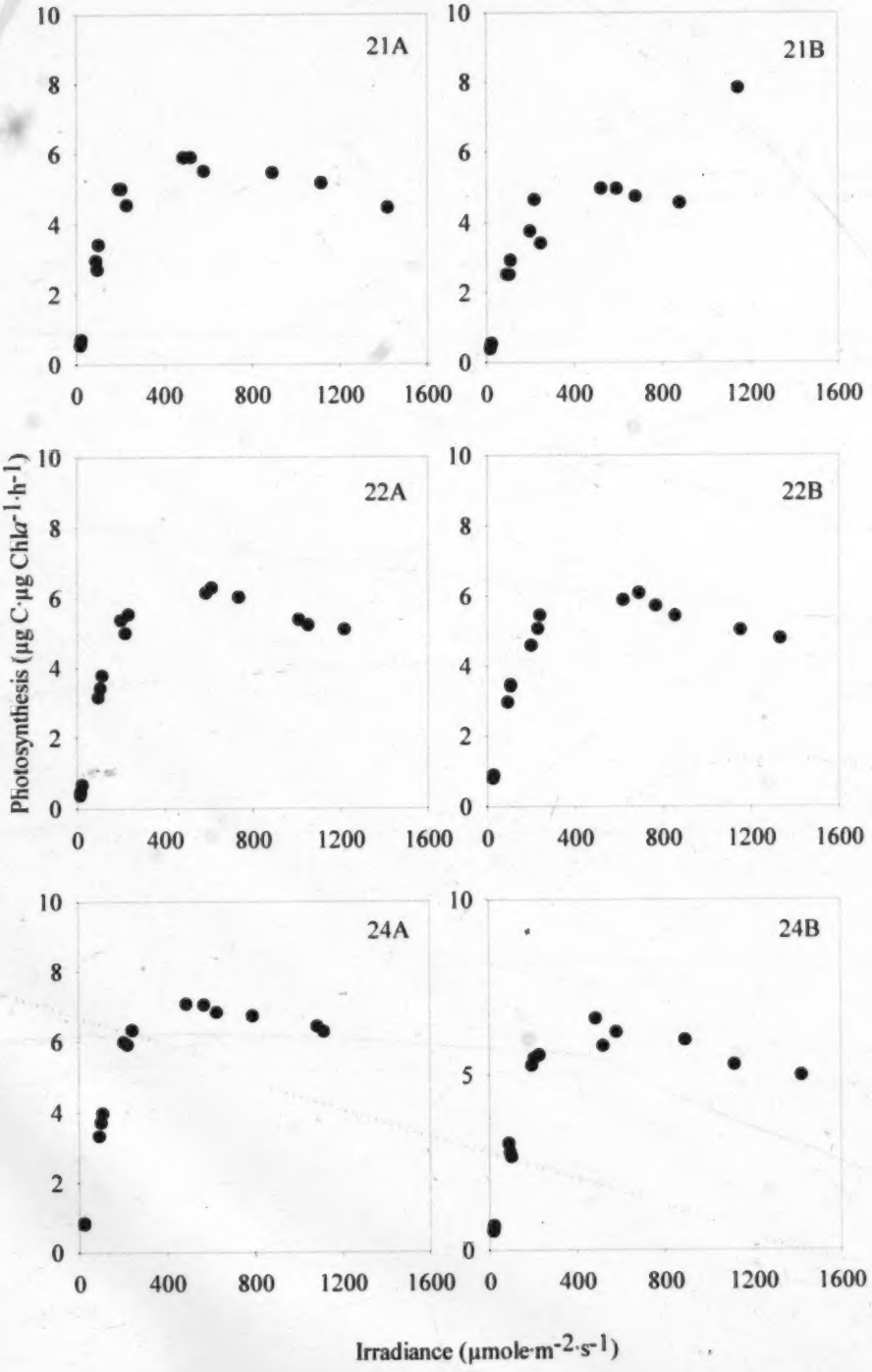


Figure C10: Phytoplankton photosynthesis-irradiance curves in SPH 100 (August 1998).

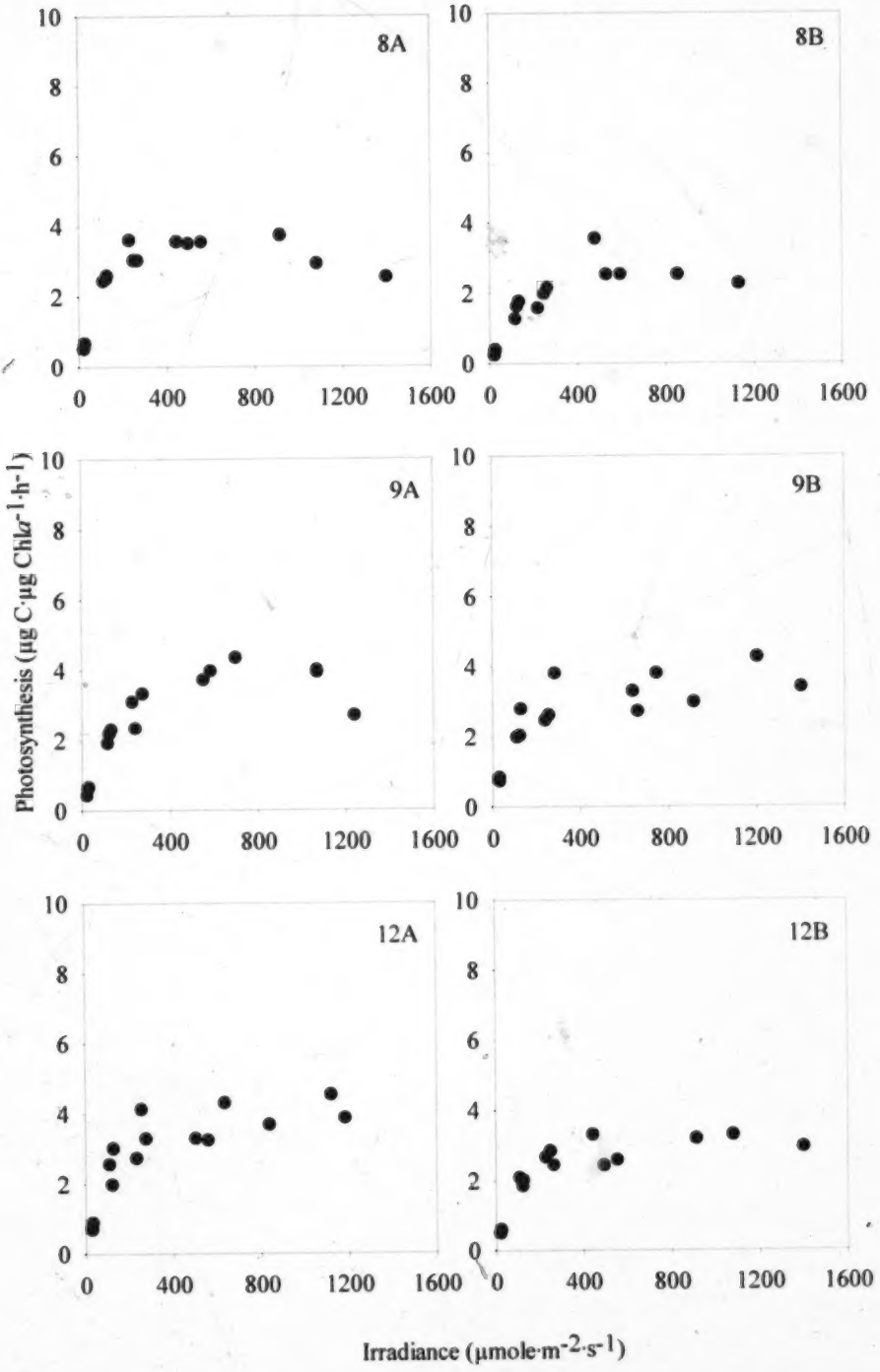


Figure C11: Phytoplankton photosynthesis-irradiance curves in SPH 200 (August 1998).

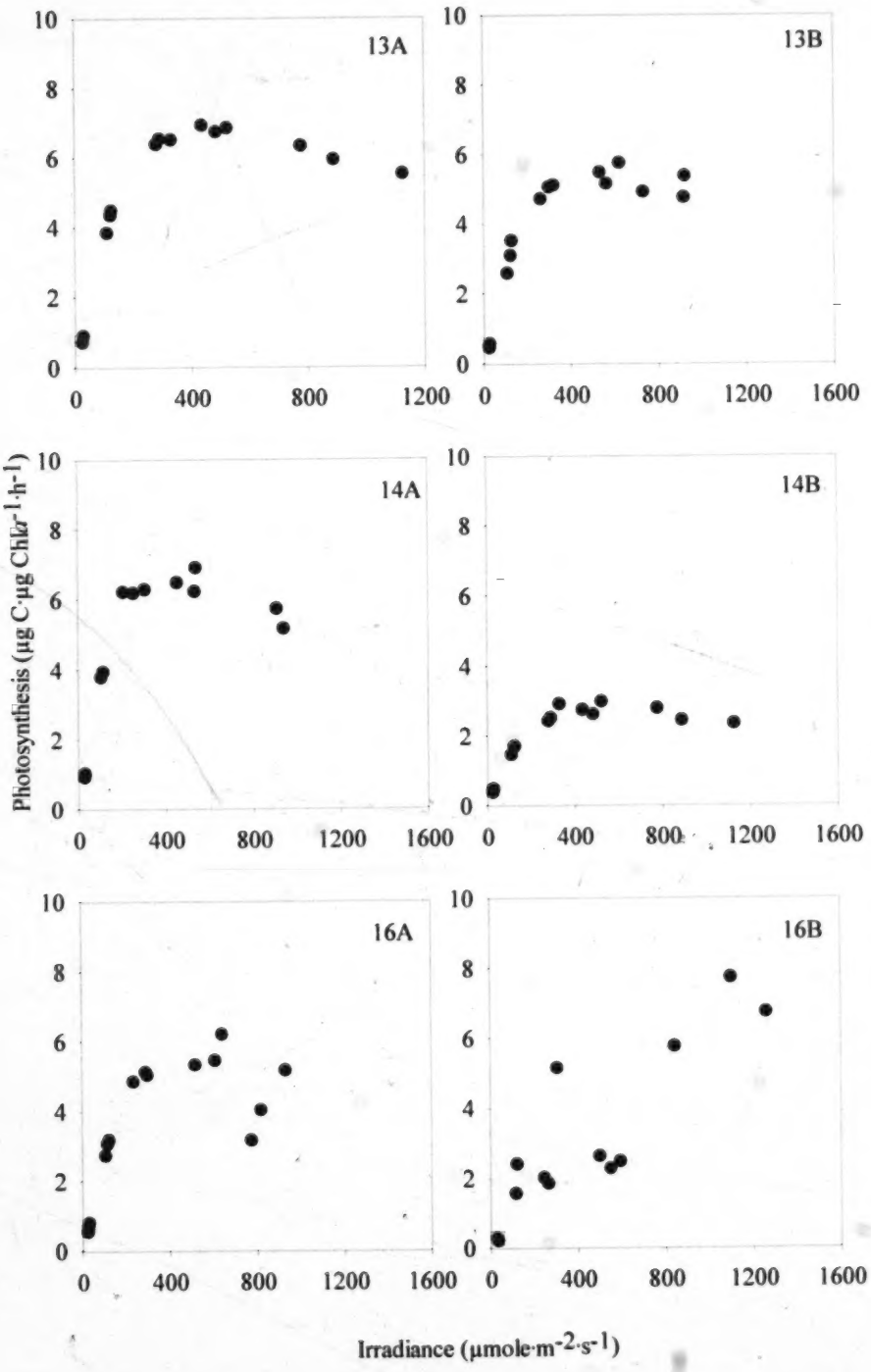


Figure C12: Phytoplankton photosynthesis-irradiance curves in SPH 800 (August 1998).

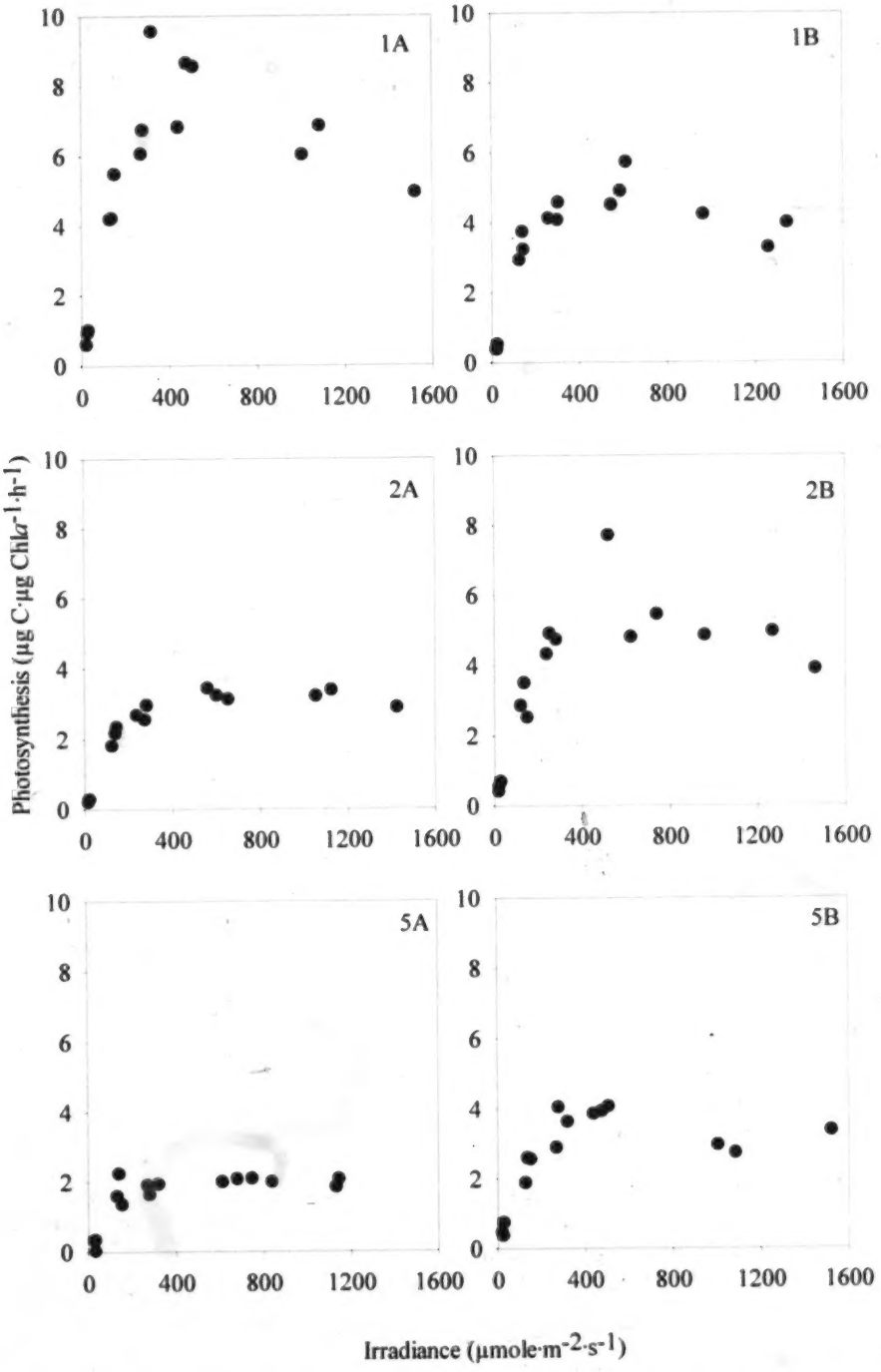


Figure C13: Phytoplankton photosynthesis-irradiance curves in SPH 20 (Septmeber 1998).

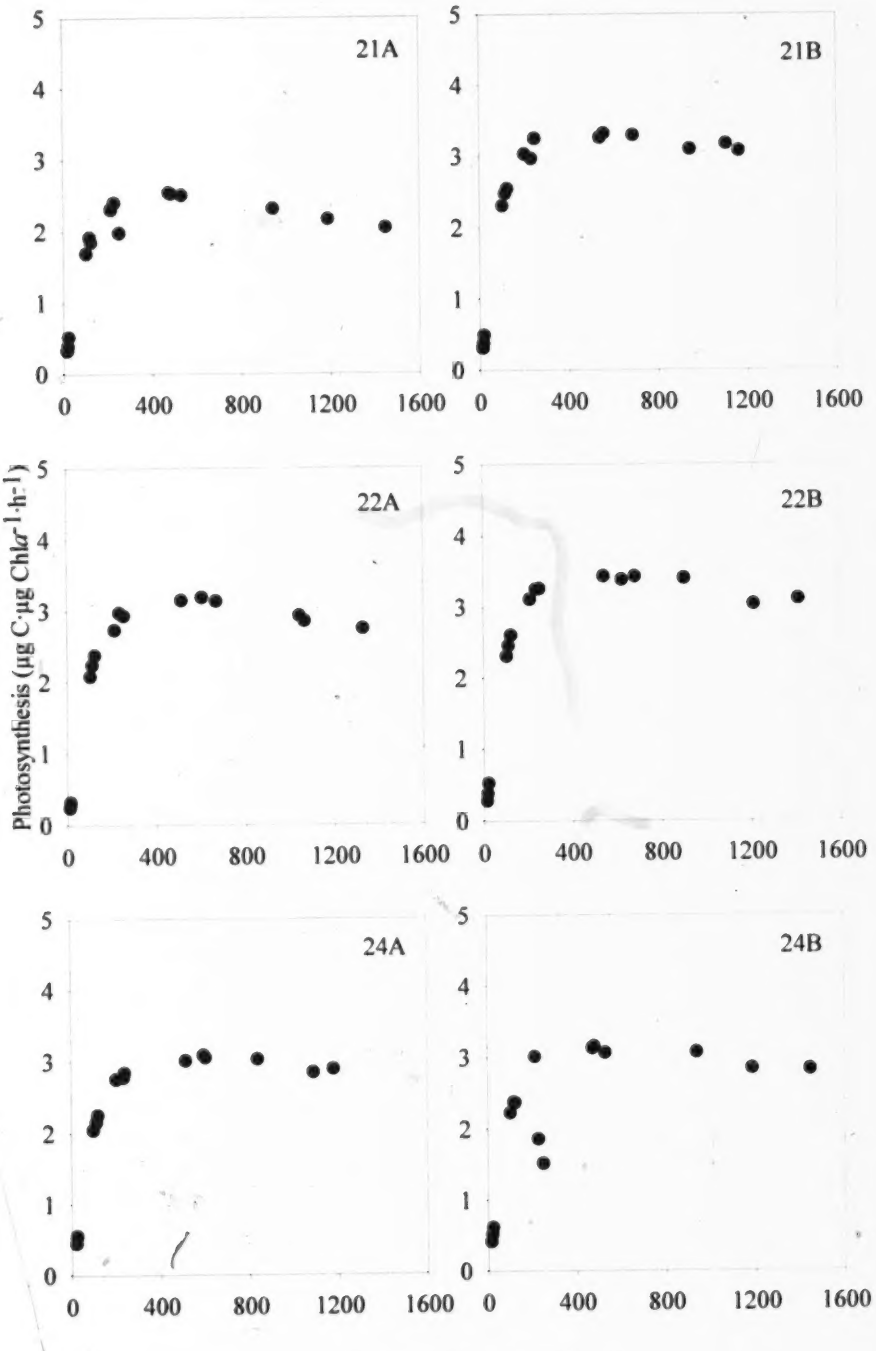


Figure C14: Phytoplankton photosynthesis-irradiance curves in SPH 100 (September 1998).

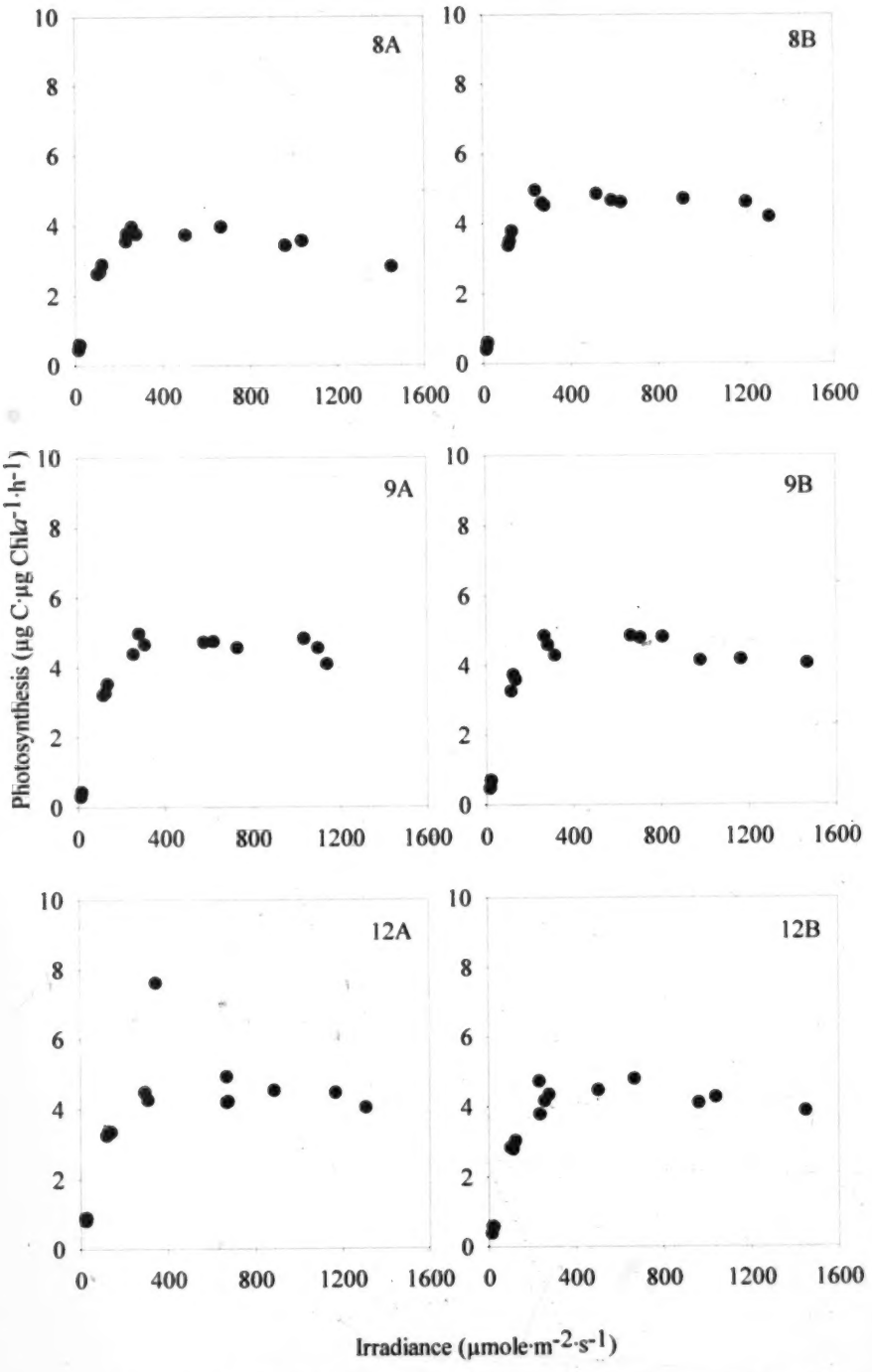


Figure C15: Phytoplankton photosynthesis-irradiance curves in SPH 200 (September 1998).

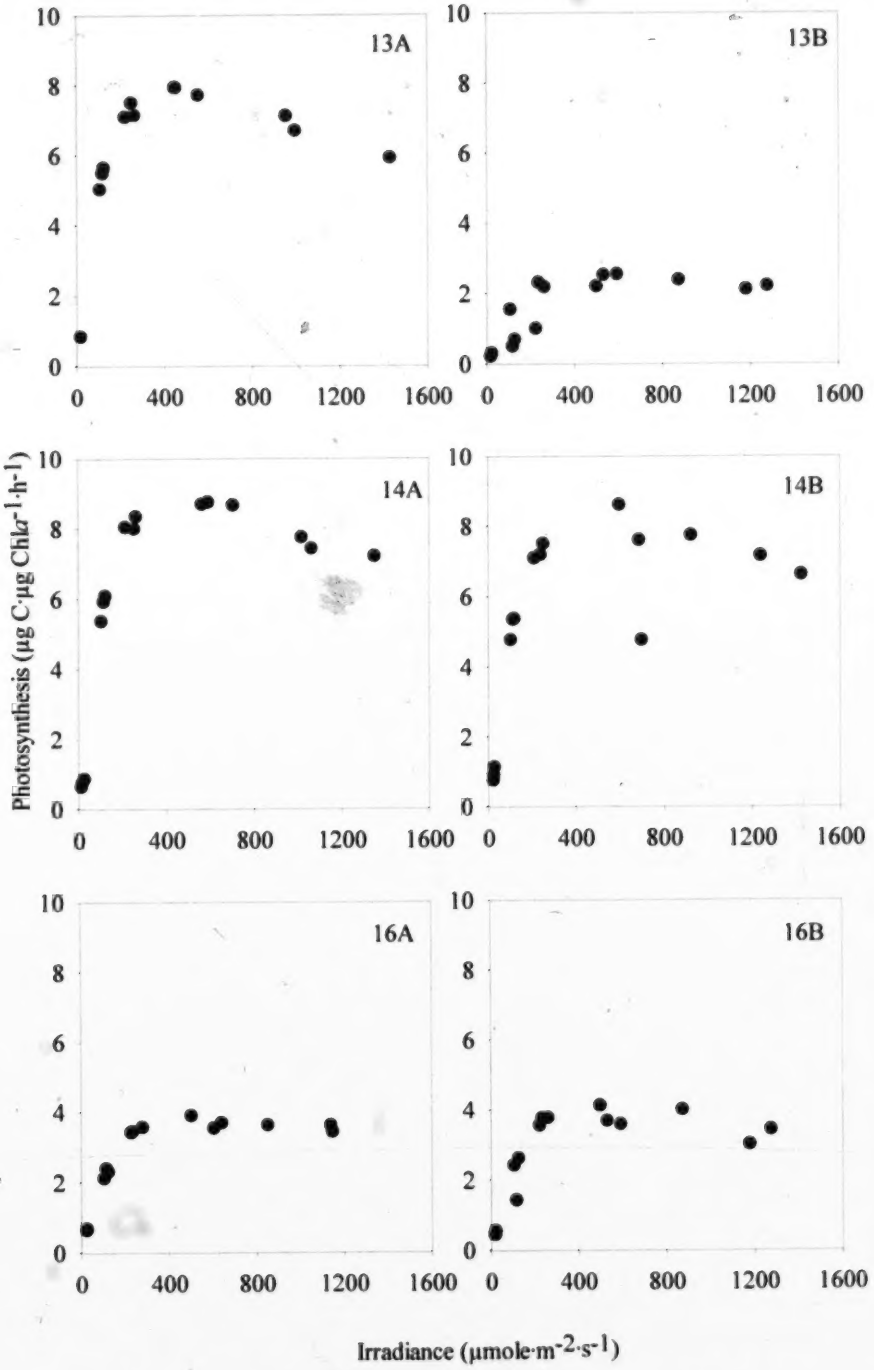


Figure C16: Phytoplankton photosynthesis-irradiance curves in SPH 800 (September 1998).